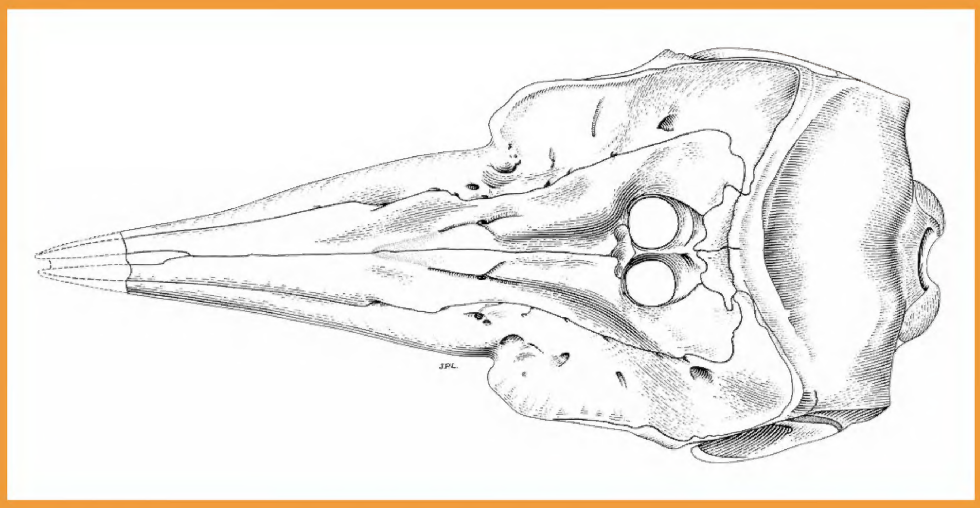
Geology and Vertebrate Paleontology of Western and Southern North America

Edited By Xiaoming Wang and Lawrence G. Barnes



Contributions in Honor of David P. Whistler

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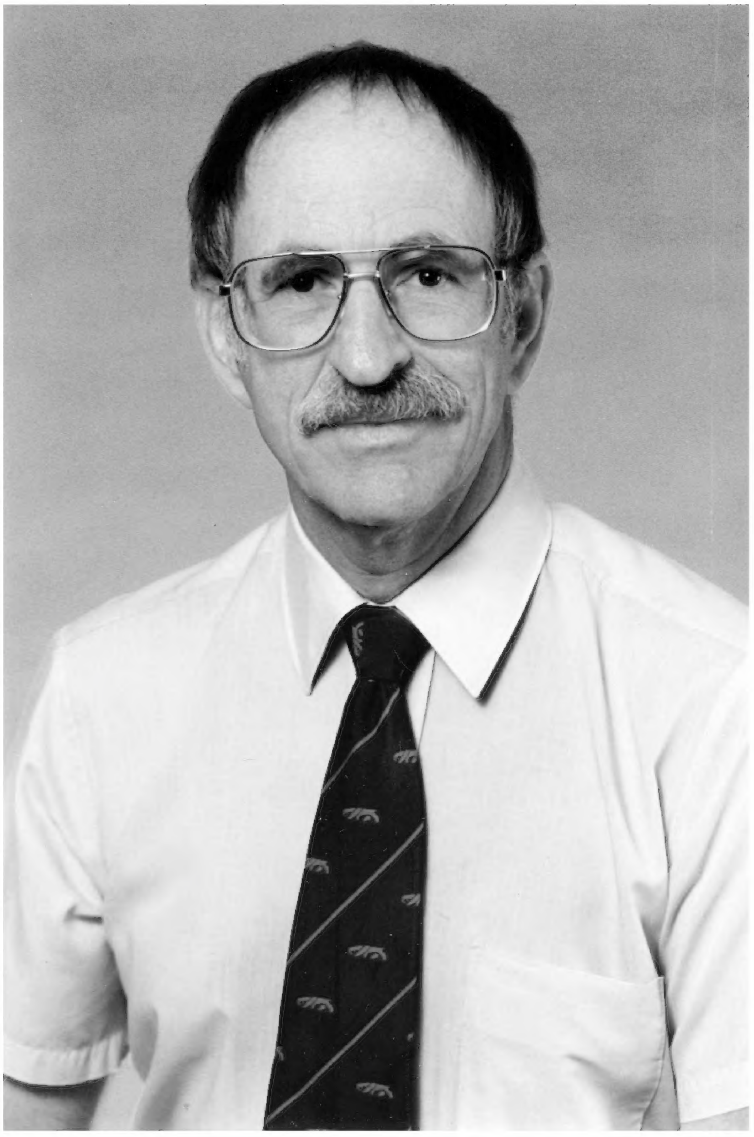
GEOLOGY AND VERTEBRATE PALEONTOLOGY OF WESTERN AND SOUTHERN NORTH AMERICA, CONTRIBUTIONS IN HONOR OF DAVID P. WHISTLER



Photograph, Dick Meier

David Paul Whistler, Curator Emeritus, Natural History Museum of Los Angeles County.

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Edited By
Xiaoming Wang and Lawrence G. Barnes

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PREFACE

The idea of a Festschrift to honor the career of Dr. David P. Whistler arose in August 2002, shortly after Xiaoming Wang joined the staff of the Natural History Museum of Los Angeles County. Our initial solicitation of manuscripts was met with enthusiasm, a testimony of Dave's popularity, and we thank our contributors for their patience and commitment in bringing this volume to fruition.

During production of this volume, we have enjoyed the support and collaboration of numerous colleagues, personal, and professional friends and associates of Dave Whistler and his wife Helen and from environmental assessment companies. We are grateful for the following individuals whose generous contributions have helped to defray the cost of printing this volume: Walter C. and Patricia L. Bauer, Ann M. Cantrell, Billy and Toni Colbert, Ted Connors, W.S. and Janet W. Cornyn, Donna Dameron, William H. Evans, Sarah and Robert Feinerman, Shirley Hoggatt, Barbara J. Hogue, Sylvia and Aisha Khan, Doris M. King, James E. and Sally Klein, Carole Kramer, Tani Sakler Krouse, Aiko Anne Kurosumi, Elaine O. Leventhal, Janice M. Lipeles, Donna Matson, Samuel A. McLeod, Elone L. Miller, Wade E. Miller, Beverly H. Nairne, Judy and Ron Perlstein, Isabel J. Rosenbaum, and Roscoe and Virginia Schaffert. We also thank the following private companies for their financial support: Paleo Environmental Associates, Inc.; LSA Associates, Inc.; and Jones and Stokes.

External reviewers have greatly improved the quality of this volume. We thank the following reviewers for their time and efforts: L. Barry Albright, III, Anthony D. Barnosky, Christopher J. Bell, Annalisa Berta, Donna Dameron, Susan D. Dawson, Jaelyn J. Eberle, Lawrence J. Flynn, Philip D. Gingerich, Jonathan H. Geisler, James L. Goedert, Stephen Godfrey, Timothy H. Heaton, Robert M. Hunt, Jr., John P. Hunter, Gerry de Iuliis, Louis L. Jacobs, Thomas S. Kelly, E. Bruce Lander, Jason A. Lillegraven, Everett H. Lindsay, Ernest L. Lundelius, Jr., Zhexi Luo, Bruce J. MacFadden, Ross D.E. MacPhee, Larry D. Martin, H. Gregory McDonald, Samuel A. McLeod, James I. Mead, Ellen J. Moore, Douglas Morton, Neil D. Opdyke, Bruce M. Rothschild, Eric Scott, Christopher A. Shaw, Gary Springer, Joe D. Stewart, Darren Tanke, Richard H. Tedford, Howell W. Thomas, Mark D. Uhen, Hugh M. Wagner, C. Sue Ware, S. David Webb, Thomas E. Williamson, and Michael O. Woodburne, as well as three anonymous reviewers. We also thank members of the Scientific Publications Committee at the Natural History Museum, Brian V. Brown, Kenneth E. Campbell, John M. Harris, and Joel W. Martin for their guidance and encouragement and for their time spent reviewing such a large volume of papers. Finally, we wish to thank our Managing Editor, Karen V. Brown, who assumed a task of this size with diligence, professionalism, and a cheerful disposition.

We express our special gratitude to three of our outstanding volunteers at the Natural History Museum, Helena Bowman, Donna Dameron, and Carole Kramer. Ms. Dameron cheerfully assumed the task of editing and checking references for the entire volume, and Ms. Kramer and Ms. Bowman were instrumental in their letter-writing campaign to help raise funds for this publication.

Xiaoming Wang
Lawrence G. Barnes
March 2007
Los Angeles, California

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Introduction

John M. Harris[1] and Lawrence G. Barnes[2]

This volume was assembled to recognize the contributions of David Paul Whistler to the profession of vertebrate paleontology, and specifically to the Natural History Museum of Los Angeles County (LACM). Much of the professional career of Dr. Whistler, or Dave, as he is known to all, has been devoted to the study of the fossil record in the Mojave Desert of Southern California. Many of the contributors to this volume are Dave's associates in studies of the same area, or in studies of other areas of California and of western North America. Many of the topics addressed in this volume resulted from work initiated, facilitated, or inspired by Dave (Fig. 1).

Dave grew up in Southern California where his initial enthusiasm and curiosity in science came from exploring his own backyard. Like several other professional vertebrate paleontologists, including Malcolm C. McKenna, Richard H. Tedford, Lawrence G. Barnes, H. Gregory McDonald, Michael J. Novacek, James Clark, and Mark Norell, Dave frequently visited the LACM as part of his elementary and high school student programs, and when he was in junior high school, he began participating in Miss Gretchen Sibley's science programs at the museum.

After high school, Dave enrolled in the Department of Physical Sciences at the University of California, Riverside, with a chemistry major. However, Dr. Richard H. ("Dick") Tedford turned Dave on to vertebrate paleontology with a field trip to Red Rock Canyon, where Dave collected his first fossil. He subsequently transferred to the Department of Geological Sciences, where Dick Tedford became his major professor and mentor for both his bachelor's and master's degrees. Dave received an undergraduate scholarship from the LACM because of his interests in Southern California paleontology, and he wrote a bachelor's thesis on the stratigraphy and paleontology of the Goler Formation. As an undergraduate, he spent four months working for the Alaska branch of the U.S. Geological Survey doing helicopter support mapping of the McCarthy Quadrangle in the Wrangell Mountains of Alaska. One day, while perched on a remote ridge eating lunch, he picked up a bone fragment, possibly of an ichthyosaur, and discovered the first Mesozoic vertebrate fossil ever found in Alaska.

Dave's master's thesis (Whistler, 1965) was about an interesting assemblage of Hemingfordian mammals from deposits that were being exploited by the boron mines in the Mojave Desert. Such mines had been made famous by the 20-mule teams that hauled borax out of Death Valley. His thesis work provided him with a foundation in the Tertiary vertebrate paleontology of the Mojave Desert, which was to be the main focus of his subsequent career.

However, Dave's paleontological interests have always been diverse, and in 1964, while he was in the throes of finishing his master's thesis, he and fellow graduate student George T. Jefferson answered the call of Dr. Frank H. Kilmer, of Humboldt State College, to check a marine fossil–producing area on Isla Cedros, a desert island off the west coast of Baja California, Mexico. In the summer of 1964, Dave and George spent several weeks on the island collecting some of the most completely preserved fossil marine vertebrate skeletons that have ever been recovered, resulting in the later recognition of several species new to science. The results of this first field season by Whistler and Jefferson, particularly their recovery of pinniped carnivorans (Repenning and Tedford, 1977), so pleased their professor, Dick Tedford, that the following year he accompanied his two energetic graduate students to collect more. The specimens amassed during those two field seasons established the assemblage as a standard of comparison for marine vertebrate assemblages of its age (Barnes, 2008) and included three new species of birds (Howard, 1971) and eight new species of marine mammals, among which was an unusual dolphin named in Dave's honor—*Albireo whistleri* Barnes, 1984.

It was at Riverside that Dave met and married Helen Moore. After completing his master's degree in geology in 1965, he was accepted into the doctoral program in paleontology at the University of California, whereupon he, Helen, and their daughter, Jennifer, moved to Berkeley. Dave's supervising professor at Berkeley was the late Dr. Donald E. Savage, and Dave became one of the more active graduate students in the Department of Paleontology. He worked as a teaching assistant and laboratory preparator,

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Figure 1 David P. Whistler is widely known for his active field work in California's Mojave Desert, characteristically striking out in new directions in avid search for new geologic and paleontologic information. Photograph by Xiaoming Wang, 2003.

participated in many departmental seminars, organized departmental picnics and parties, and did a lot of fieldwork. With fellow graduate student J. Howard Hutchison, he cofounded *PaleoBios,* the publication of the Museum of Paleontology. Dave's first scientific paper was also the first issue of *PaleoBio*s (Whistler, 1967), describing oreodonts from the Tick Canyon Formation, a rock unit he first explored while a master's student at Riverside. During their time in Berkeley, Dave's second daughter Cheryl was born. Both Jennifer and Cheryl went on to earn doctorate degrees in molecular biology.

Dave's doctoral research continued to follow his interest in the vertebrate paleontology and stratigraphy of the Mojave Desert—a study of the microvertebrates and their stratigraphic distribution within the late Miocene Dove Spring Formation, which was then known as the Ricardo Formation. His Ph.D. dissertation (Whistler, 1969) was titled "Stratigraphy and small fossil vertebrates of the Ricardo Formation, Kern County, California." Dave's work on this rock unit and its fossil content (Fig. 2) was directly influenced by, and a continuation of, the work of his former mentor Dick Tedford, who at about that time left Riverside for the American Museum of Natural History in New York. Dave's research was also in the tradition of the pioneering work of John C. Merriam, Chester Stock, Eustace L. Furlong, and Daniel I. Axelrod, who had at various times also been at Berkeley, undertaken field work in the Ricardo Formation, and published on its fossils. It culminated in a major contribution that included the geochronology and magnetostratigraphy of the Dove Spring Formation (Whistler and Burbank, 1992). As a result, the Dove Spring Formation has become the

Figure 2 In the Red Rock Canyon area, the Neogene Dove Spring Formation includes several layers that contain mammal footprint impressions, evidence that earlier land life in California's Mojave Desert was much different than it is now. Here, Dave Whistler works to expose the trackway of a large late Miocene camel. Photograph by Xiaoming Wang, 29 April 2005.

standard of comparison for Clarendonian and early Hemphillian land mammalian assemblages of western North America.

In 1968, after completing his doctoral course work at Berkeley, Dave was hired as an assistant professor of Geology at Texas Tech University in Lubbock. He taught there for an academic year before he was offered the position of senior curator of Vertebrate Paleontology at the LACM on the basis of his expertise in the geology and paleontology of Southern California. Dave held that post for more than 30 years.

During his career at LACM, Dave served for 14 years as the section head of Vertebrate Paleontology and deputy division chief for Earth Sciences, and he was acting head of the Earth Sciences Division from 1979 to 1980. He served on numerous museum committees and was instrumental in the design of several exhibits. He was a member of the Council of Environmental Quality and Systematics Collections of the Association of Systematics Collections from 1973 to 1978 and was a member of the board of directors and chairman of the Publication Committee of the Southern California Academy of Sciences from 1973 to 1977. He was a very active member of the Society of Vertebrate Paleontology, serving as secretary/treasurer from 1984 to 1990, and also serving on the Committee on Data Standards and Electronic Data Processing (1972–1973), Government Liaison Committee (1973–1978), Endowment Committee (1984–1993), Conformable Mitigation Committee (1989–2002), and Ethics Committee (1991–1995). He organized museum field programs for members, families, and students, and by leading field trips and helping to judge science fairs, he gave years of devoted service to school programs similar to the one that originally brought him to the museum.

In his role as senior curator of Vertebrate Paleontology, Dave was the principal investigator of two National Science Foundation (NSF) collection care grants, the first of which (1972–1977) was the largest NSF grant that the museum had received up to that time and which addressed needs in the curation of the collections. The second grant (1983–1986) continued the curation of the collections and expedited their computerization. As far as research, Dave documented 777 localities in 20 Californian formations that range

Figure 3 Dave Whistler at work at a heavy liquid flotation facility he constructed at the Natural History Museum of Los Angeles County to assist in separating small vertebrate fossils from residual sediment, following underwater screen washing. Dave's labors using this process yielded many new records of small vertebrates from several Southern California deposits. Photograph by Dick Meier, probably in the 1980s.

in age from Eocene to late Pleistocene. He specialized in what he called "little critters," and was on the forefront of refining microvertebrate collecting techniques, including developing and fine-tuning heavy liquid flotation techniques using sodium polytungstate, a concept he borrowed from the oil industry. In addition to the facility at the LACM (Fig. 3), Dave had a similar setup of his own at home in Van Nuys, including a screening machine. Because the process of concentrating the fossil-bearing fraction of a rock sample involved the use of citrus oil to disperse and remove the clay fraction, Dave's neighbors occasionally remarked how fragrant his yard was! A large percentage of the more than 10,000 specimens, of which he was the primary collector, comprise tiny teeth and jaws of rodents and reptiles that he personally mounted on pins for study and stored in small glass vials (Fig. 4). We can only speculate as to how many tons of matrix Dave and his field assistants packed in from the field to be washed, screened, and sorted in this effort. However, his interests remained wide reaching, and the last manuscript that he wrote as a curator (with David Webb) described what was for decades informally known as "*Huatherium*," a new late Pliocene goatlike camel from Tecopa Lake near California's Death Valley (Whistler and Webb, 2005).

Among Dave's other notable accomplishments are those he achieved while working with other vertebrate paleontologists in Southern California, particularly those who are employed as environmental consultants involved with mitigating the effects of major construction projects on paleontologic resources (e.g., Lander, 2008) and those concerned with their own research projects. His efforts always included the heavy-liquid separation of fossil-bearing concentrate, generated by wet screening large samples of rock, and identification of the recovered microvertebrate remains, particularly rodent teeth. Largely on the basis of Dave's rodent identifications, the ages of the various horizons within the Sespe Formation, for example, have been established with much greater accuracy, making it possible to correlate

Figure 4 The Natural History Museum of Los Angeles County conserves significant collections of small vertebrates from diverse late Cenozoic deposits of western North America. Here, Dave Whistler curates a collection of such fossils, many of which are mounted on the heads of pins, attached to corks, and inserted into glass vials. Photograph by Dick Meier, ca. 1985.

strata between stratigraphically superposed geographically widely separated areas. Dave was the first to recognize the occurrences of rodent assemblages of late Uintan, Arikareean, and early Hemingfordian age in the northern Santa Ana Mountains of Orange County and subsequently was the first to document correlative, taxonomically similar assemblages of Arikareean and early Hemingfordian age in the central Santa Monica Mountains of Los Angeles County, and of early Arikareean age along the southern side of Simi Valley in Ventura County. Many publications were generated by Dave's findings but only in some instances was he listed as a coauthor. For example, his findings are the foundation for the contribution about the Sespe Formation by Calvano et al. in this volume. Dave's work on the rodents from the Lake Mathews Formation of western Riverside County (Lander and Whistler, 2002) and his published work on the rodents and larger land mammals from the Dove Spring Formation (Whistler and Burbank, 1992) likewise are major components of Lander's contribution to this volume on the Lake Mathews Formation.

Dave's long-term field project at Red Rock Canyon exemplifies his contribution to the discipline. Over the course of his career, he identified 707 localities in the Red Rock Canyon area, and these yielded more than 6,200 specimens, more than 3,800 of which he was personally involved in collecting. The paleontologic and geologic studies in this area generated 17 of his publications. In addition to his own collecting trips, for many years, Dave led an annual Memorial Day weekend pilgrimage to Red Rock Canyon for the volunteers of the George C. Page Museum lab, exposing them to more standard (nonasphaltic) paleontological collecting procedures. Many, like Eric Scott and Gary Takeuchi, who later became professional paleontologists, received their initial field training in this manner. Dave worked very closely with private collectors such as Beth Chassée, Jack and Marian McConnell, and Harry Quinn, all of whom have contributed some very important specimens to the collections. Dave also led a very successful Earth Watch project to this location, and in the last eight years of his career at the museum, he collaborated extensively with the Education Division offering paleontological orientated programs for families and children (Fig. 5). "Dr. Dave's" weekend collecting trips

Figure 5 Dave Whistler led many trips to the Mojave Desert for the Membership and Education programs of the Natural History Museum of Los Angeles County, as well as for other educational organizations. Here, in Red Rock Canyon State Park, he is lecturing about geology atop Whistler Ridge, named in his honor by California State Park employees. Photograph by Dick Meier, probably in the late 1990s.

to Red Rock Canyon for museum members, featuring Helen's gourmet camp catering, quickly sold out whenever they were offered, a tribute to his talent for sharing the adventure and excitement of paleontologic and geologic discoveries.

As an outgrowth of his fieldwork, Dave worked extensively with Ranger Mark Faull and the California State Parks Department in developing the Interpretive Center, exhibits, and educational programs at Red Rock Canyon State Park, which encompasses much of the Dove Spring Formation. Following his retirement from the museum, Dave has continued his work with the State Park and with the LACM as curator emeritus. In 2000, he received the California State Parks DeWitt award for partnership, and recently, Whistler Ridge was named in his honor (Fig. 5).

In addition to Dave's museum-related fieldwork, curation, and research, he has left his mark on California with the writing of many technical reports that are related to the mitigation of impacts to fossil resources. Not only did he help build the extensive vertebrate paleontology collection of the LACM, he made it accessible to his peers and generated an interest and an excitement about the importance of vertebrate paleontology to people of all ages. We are all grateful for his extensive contributions on behalf of the museum and the Department of Vertebrate Paleontology.

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Paleocene primates from the Goler Formation of the Mojave Desert in California

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ABSTRACT. Recent collecting efforts in the Goler Formation in California's Mojave Desert have yielded new records of turtles, rays, lizards, crocodilians, and mammals, including the primates *Paromomys depressidens* Gidley, 1923; *Ignacius frugivorus* Matthew and Granger, 1921; *Plesiadapis* cf. *P. anceps*; and *Plesiadapis* cf. *P. churchilli*. The species of *Plesiadapis* Gervais, 1877, indicate that Member 4b of the Goler Formation is Tiffanian. In correlation with Tiffanian (Ti) lineage zones, *Plesiadapis* cf. *P. anceps* indicates that the Laudate Discovery Site and Edentulous Jaw Site are Ti2–Ti3 and *Plesiadapis* cf. *P. churchilli* indicates that Primate Gulch is Ti4. The presence of *Paromomys* Gidley, 1923, at the Laudate Discovery Site suggests that the Goler Formation occurrence is the youngest known for the genus. Fossils from Member 3 and the lower part of Member 4 indicate a possible marine influence as Goler Formation sediments accumulated. On the basis of these specimens and a previously documented occurrence of marine invertebrates in Member 4d, the Goler Basin probably was in close proximity to the ocean throughout much of its existence. Member 4 of the Goler Formation was deposited primarily by rivers that contained a diverse assemblage of turtles and mammals, with lizards, crocodilians, and particularly fish being rarer. An abundance of fossil wood in Member 4 suggests that Goler primates lived within stands of trees adjacent to the rivers. The Goler Formation provides the only diverse sample of Paleocene continental vertebrates from the west coast of North America. Goler mammalian assemblages are generally similar to Tiffanian faunas from the Rocky Mountain states; therefore, generally favorable conditions for dispersal between the coast and western interior must have existed. However, significant endemism is also evident in that Goler specimens of *Plesiadapis* cannot confidently be referred to existing species, and some new species of turtles and mammals are present in Goler vertebrate assemblages.

INTRODUCTION

The Goler Formation crops out in the El Paso Mountains in the southwestern Great Basin in the Mojave Desert of California (Fig. 1). It is immensely thick, more than 3 km, and is subdivided into four members (Fig. 2) comprising mainly fluvial deposits (Dibblee, 1952; Cox, 1982, 1987), although the uppermost member contains a thin interval of marine sediments (Cox and Edwards, 1984; Cox, 1987). Originally, Goler sediments were thought to be late Eocene to Miocene in age on the basis of fossil plants (Axelrod, 1949) and other evidence (Dibblee, 1952).

The first vertebrate data potentially useful in determining the age of the Goler Formation came in 1950 when a turtle carapace and mammal tooth were found by Richard H. Tedford and R. Shultz in Member 3. They took the fossils to Chester Stock at the California Institute of Technology, but unfortunately, before the specimens could be studied, Stock died, and the fossils were lost. However, soon thereafter, M. McKenna collected a periptychid mammal jaw fragment at the Laudate Discovery Site (base of Member 4b), which is higher in the section than the Tedford-Schultz site. This discovery indicated a Paleocene age for this part of the formation (McKenna, 1955). Over the next 35 years only about a dozen identifiable vertebrate specimens were found (all but one from Member 4a and 4b), but they corroborated the Paleocene age (McKenna, 1960; West, 1970; McKenna et al., 1987). More specifically, the mammalian fauna from Member 4b suggested that this part of the Goler Formation was Torrejonian or early

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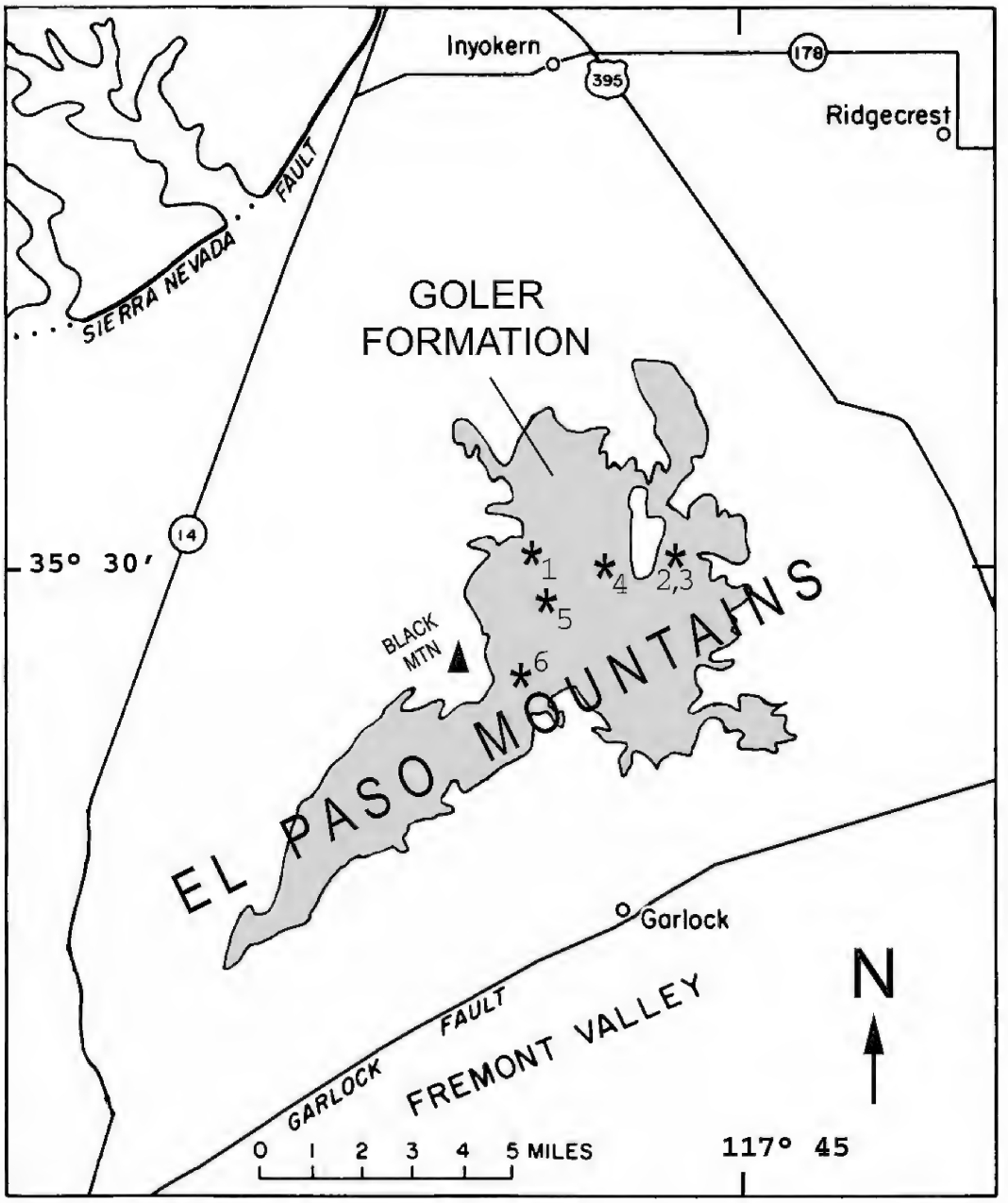

Figure 1 Outcrop map of the Goler Formation (shaded), with major vertebrate sites numbered; see Figure 2 for site names and Figure 3 for location of the El Paso Mountains within California; map adapted from Cox (1987).

Tiffanian in age (McKenna, 1960; McKenna et al., 1987).

By 1990, the Goler Formation was widely recognized as being critically important in elucidating California's early Cenozoic history. It was the only known Paleocene rock unit on the west coast of North America that could potentially yield a diverse assemblage of fossil vertebrates. Accordingly, field crews from the Raymond M. Alf Museum of Paleontology and other institutions initiated a long-term effort in 1993 to recover a large sample of Goler vertebrates, primarily through the use of screen-washing techniques. Important new mammal localities were discovered, both lower and higher in Member 4 than the original Laudate Discovery

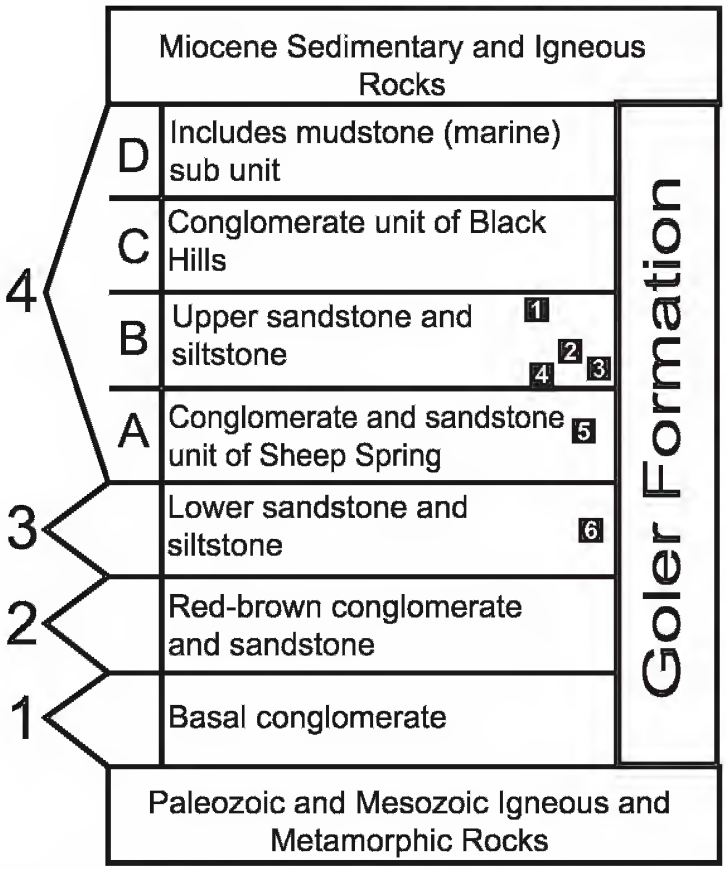

Figure 2 Stratigraphic subdivision of the Goler Formation showing the four members and subdivisions of Member 4 (after Cox, 1987), with approximate stratigraphic location of major vertebrate-yielding sites numbered as **1**, Honey Pot, locality V200120; **2**, Primate Gulch, locality V200202; **3**, Edentulous Jaw Site, locality V98012; **4**, Laudate Discovery Site, locality V94014; **5**, Land of Oz, locality V20001; and **6**, the Tedford-Shultz Site. See text for discussion of stratigraphic relations between sites 2 through 4.

Site (Fig. 2). More than 15 tons of sediment were screen-washed, and a few hundred additional specimens were recovered. Many species represent new records for the Goler Formation, including several kinds of turtles (baenids, "macrobaenids," and trionychids), rays (cf. *Hypolophodon* Capetta, 1980), lizards (cf. *Proxestops* Gauthier, 1982; cf. *Paleoxantusia* Hecht, 1956), crocodilians (cf. *Allognathosuchus* Mook, 1921), and mammals (multituberculates, marsupials, plesiadapid and paromomyid primates, carnivores, and mesonychids, as well as arctocyonid, hyopsodontid, phenacodontid, and periptychid ungulates) (Lofgren et al., 1999, 2002, 2004c; McKenna and Lofgren, 2003). The newly expanded assemblage of mammals is diverse and represents the oldest known record of Mammalia from California other than the metacarpal recently described from late Cretaceous marine rocks in Butte County (Wilson et al., 2003). The Goler Formation specimens are also the oldest mammalian dental remains from the west coast of North America other than the few specimens described by Lillegraven (1972, 1976) from Upper Cretaceous rocks of Baja California.

Of particular interest is the recovery of the primates *Plesiadapis, Ignacius* Matthew and Granger, 1921, and *Paromomys*. Their occurrence in California during the Paleocene raises interesting paleoecological and paleobiogeographic issues. The nearest sites that have yielded *Plesiadapis* are in Colorado and Wyoming (Fig. 3). Also, the presence of *Plesiadapis* indicates that the mammal-bearing part of Member 4 is younger than was previously thought. Here we describe California's first record of Paleocene primates, their utility in determining the age of the mammal-yielding part of the formation, and implications of their presence to Paleocene paleobiogeography and paleoecology of this part of western North America.

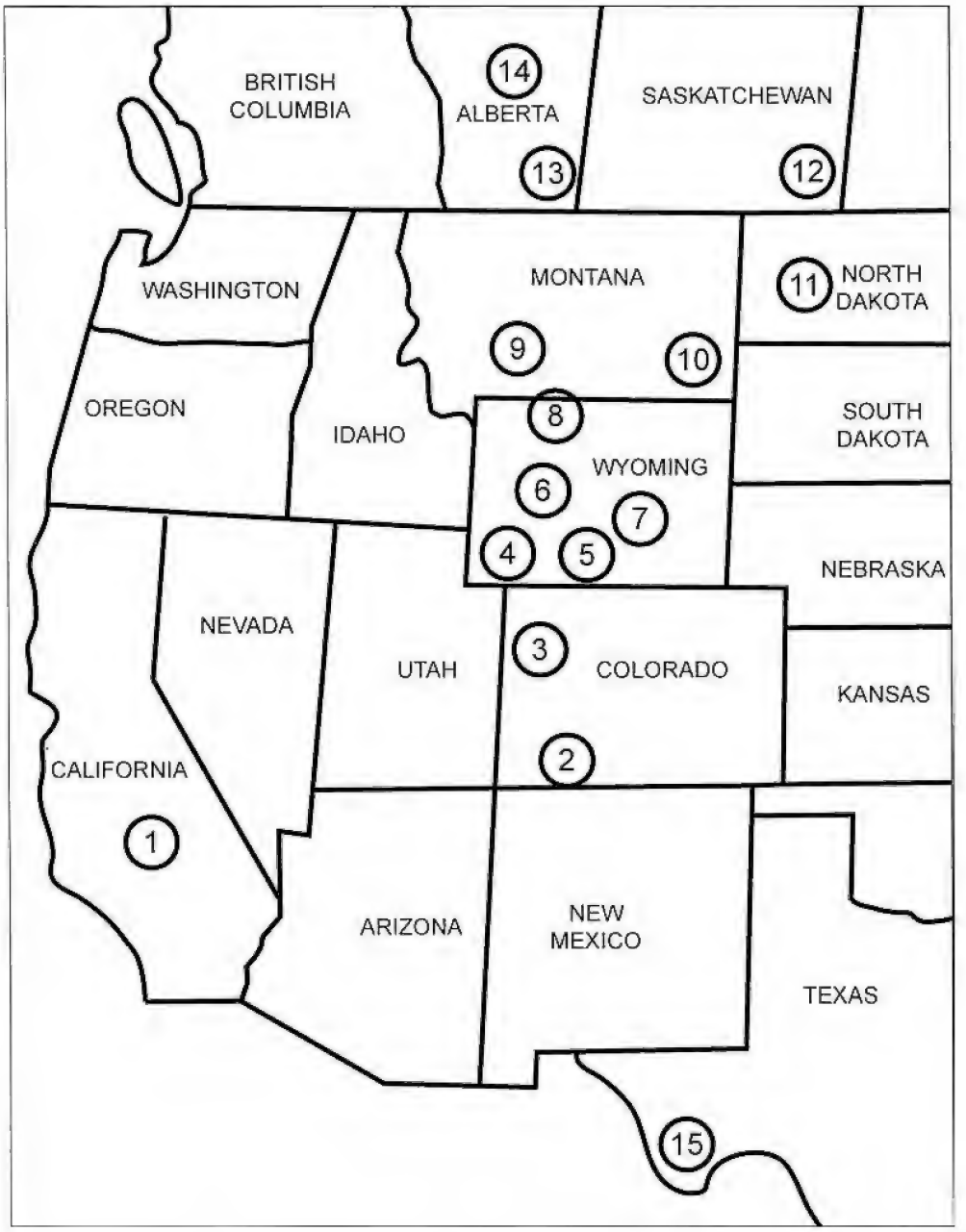

Figure 3 Map of western North America with areas (basins, formations, or localities) that have yielded Paleocene plesiadapids: **1**, Goler Formation; **2**, Animas Formation; **3**, Piceance Creek Basin; **4**, Green River and Fossil basins; **5**, Washakie and Bison basins; **6**, Wind River and Hoback basins; **7**, Hanna and Carbon basins; **8**, Bighorn and Clarks Fork basins; **9**, Crazy Mountains Basin; **10**, Western Williston and Powder River basins; **11**, Eastern Williston Basin; **12**, Roche Percée; **13**, Police Point; **14**, Paskapoo and Porcupine Hills formations; and **15**, Blacks Peak Member of Tornillo Formation. Adapted from Gingerich (1976).

METHODS AND MATERIALS

Primates described here were recovered from three sites: (A) V200202, Primate Gulch, RAM 7193; (B) V98012, Edentulous Jaw Site, RAM 6431, 6433, 6446, 6700, 6929, 6931, 6934, 6935, 6946, 6957, 6960, 6961, 6962, 6963; and (C) V94014, Laudate Discovery Site, RAM 6426,

6925. RAM 6925 and 7193 were found by surface collecting. All of the others were recovered through the screen-washing process. The classification scheme used here follows that of McKenna and Bell (1997). An ocular micrometer (RAM 7193) and digital calipers (all other specimens) were used to measure teeth. Measurements are in millimeters. Cusp terminology for teeth is that of Van Valen (1966:fig. 1) and Gingerich (1976:figs. 4 and 5). Measurements of teeth were taken following Lillegraven (1969:fig. 5). For plesiadapid upper incisors, maximum width was measured at the widest part of the laterocone, perpendicular to the long axis of the tooth.

The Raymond M. Alf Museum of Paleontology (RAM) records each vertebrate locality with a V followed by numbers (e.g., V98012). Specimens are given a numerical code preceded by RAM (e.g., RAM 6925).

ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York USA
GH Wa	Geiseltalmuseum, Halle, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts USA
PU	Princeton University (now at Peabody Museum, Yale University), New Haven, Connecticut USA
RAM	Raymond M. Alf Museum of Paleontology, The Webb Schools, Claremont, California USA
SMM	Science Museum of Minnesota, St. Paul, Minnesota USA
UA	University of Alberta, Calgary, Alberta Canada
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
USNM	Department of Paleobiology United States National Museum, Smithsonian Institution, Washington, D.C. USA

SYSTEMATICS

Order Primates

Suborder Dermoptera

Family Paromomyidae Simpson, 1940

Subfamily Paromomyinae Simpson, 1940

Paromomys Gidley, 1923

Paromomys depressidens Gidley, 1923
Figure 4

HOLOTYPE. USNM 9546, part of upper jaw with P4–M3, Gidley Quarry, Fort Union Formation, Montana (middle Torrejonian).

REFERRED SPECIMEN. One P4 (RAM 6426) from locality V94014.

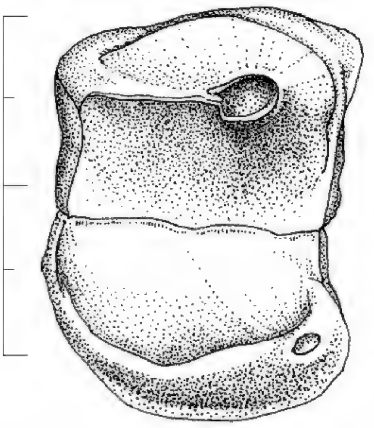

Figure 4 *Paromomys depressidens* Gidley, 1923, right P4, RAM 6426 from locality V94014, occlusal view. Scale bar = 2 mm.

DESCRIPTION. The only specimen from the Goler Formation that can be assigned to *Paromomys* is a slightly damaged P4 (RAM 6426). Damage is primarily limited to the tooth's edge as the thin veneer of enamel that should coat the tooth is absent from its posterolabial, anterolabial, and labial margins. The absence of enamel in these regions does not appear to alter significantly the tooth's general morphology, except that the small metastyle and parastyle were probably more pronounced. The paracone is large and connected to a small metastyle by a very well developed postparacrista. A metacone is not present. The protocone is less elevated and significantly smaller than the paracone, and it is positioned anterior to the paracone on the anterolingual edge of the tooth. A prominent cingulum runs posterior from the protocone, becoming progressively less developed as it curves around to the tooth's posterior edge. Between this cingulum, the protocone, and the paracone-postparacrista is a large posterolingual basin. Between the parastyle and metastyle, a buccal cingulum was almost certainly present because a distinct lineation is evident that appears to approximate the former position of the cingulum. A cingulum does not appear to have been present between the parastyle and protocone. However, owing to the lack of enamel in this region of the tooth, a cingulum could have been present, but if so, it was very diminutive. The length of RAM 6426 is 1.85 mm, width is 2.36 mm.

DISCUSSION. Gidley (1923) erected the genus *Paromomys* and named two species, *Paromomys maturus* Gidley, 1923, and *Paromomys depressidens,* both from the Gidley Quarry, Lebo Formation, Crazy Mountains, Montana. They were differentiated by size and morphology (Gidley, 1923). The type of *P. depressidens* (USNM 9546) is a right maxillary fragment with P4–M3. The P4 of the type was described as having a well-

developed posterior cingulum with a "postprotocrista" that forms with the protocone a posterolingual basin on the tooth, with an incipient metacone placed on the postparacrista near the external cingulum (Gidley, 1923). No measurements of the P4 of the type were given. However, Simpson (1937) later noted that the P4 of USNM 9546 was 1.9 × 2.0 mm (length × width) and also that the metacone of *P. depressidens* was very small or indistinct on P4 (Simpson, 1955).

RAM 6426 is referred to *Paromomys depressidens* because it is much smaller than the P4 of *P. maturus*, it lacks a distinct metacone and, although slightly larger, it is very similar in size and morphology to specimens referred to the species, especially those from the Swain Quarry, Fort Union Formation, Wyoming, described by Rigby (1980). Lack of a metacone on RAM 6426 clearly distinguishes it from *Phenacolemur* Matthew, 1915, *Ignacius*, and *Palaechthon* Gidley, 1923, all of which have distinct P4 metacones (Simpson, 1955). Compared with P4s referred to *P. depressidens* from other sites, RAM 6426 is large (1.85 × 2.36 mm), more transverse than the holotype (1.9 × 2.0 mm) from Gidley Quarry, and larger than single P4s referred to *Paromomys* cf. *P. depressidens* from Cochrane 2, Porcupine Hills Formation, Alberta (UA 11744, 1.5 × 1.8 mm) (Krause, 1978) and *Paromomys* near *P. depressidens* from the Shotgun Fauna, Fort Union Formation, Wyoming (MCZ 18764, 1.6 × 1.9 mm; Gazin, 1971). Unlike RAM 6426, the latter two specimens have a small metacone (Gazin, 1971; Krause, 1978). RAM 6426 is most similar to the Swain Quarry sample of *P. depressidens* where measurements of four P4s are presented (observed range 1.77–1.85 mm × 2.1–2.25 mm; Rigby, 1980:table 32). Also, the Swain Quarry sample is described as being inseparable from the Gidley Quarry sample from which the holotype was collected (Rigby, 1980). Specimens from the Gidley Quarry were not studied, but those from the Swain Quarry sample were compared directly with the Goler specimen. RAM 6426 is virtually identical to both AMNH 80976a and AMNH 80976b, although RAM 6426 is slightly more transverse than either AMNH specimen.

Subfamily Phenacolemurinae Simpson, 1955

Ignacius Matthew and Granger, 1921

Ignacius frugivorus Matthew and Granger, 1921

Figure 5

HOLOTYPE. AMNH 17368, left maxilla with P2, P4–M2. Mason Pocket, Animas Formation, late Tiffanian, Colorado.

REFERRED SPECIMEN. One m3 (RAM 6433) from locality V98012.

DESCRIPTION. The slightly damaged lower molar (RAM 6433) assigned to *Ignacius* is small; length 2.94 mm, width 1.47 mm. It was found in two pieces during sorting of screen-washed concentrate (the small fragments missing from the lingual and labial margins of the talonid were not recovered). RAM 6433 is slightly worn, with significant wear evident only on the paraconid and metaconid. The paraconid and metaconid are small, subequal in size, and separated by a narrow, but distinct, valley. Only after moderate to heavy wear would the paraconid and metaconid merge into a single cusp. The paraconid is deflected labially relative to the metaconid. The protoconid is the largest of the trigonid cusps, and it is connected to the metaconid by a well-developed protocristid. The paracristid is lower and less developed than the protocristid and curves at its labial edge to connect with the protoconid. The protoconid and metaconid are approximately parallel in relation to the lingual–labial axis of the trigonid. RAM 6433 has a rounded and well-developed hypoconulid lobe that is broad and elevated. The hypoconulid lobe is separated into two distinct bulbous cusps by a shallow valley. A small, slightly elevated hypoconid is present. Immediately posterior to the hypoconid, the talonid's margin deflects lingually, forming a distinct notch that separates the hypoconulid lobe from the hypoconid. A distinct entoconid is present on a well-developed and sharply elevated crest that borders the lingual margin of the talonid. The entoconid is larger and much higher than the hypoconid and is positioned more posteriorly on the talonid. A notch is not present on the lingual margin of the talonid, anterior to the hypoconulid lobe.

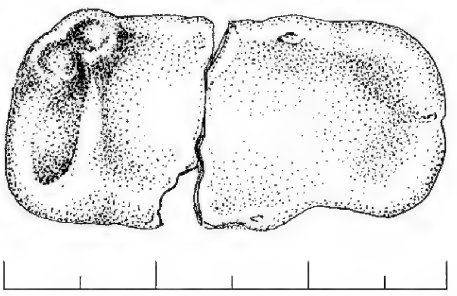

Figure 5 *Ignacius frugivorus* Matthew and Granger, 1921, left m3, RAM 6433 from locality V98012, occlusal view. Scale bar = 3 mm.

DISCUSSION. Distinguishing between species of *Ignacius* and *Phenacolemur* based on isolated teeth is difficult (Rose, 1981). Matthew's (1915) genus *Phenacolemur* was based on a lower jaw of *Phenacolemur praecox* Matthew, 1915. Soon thereafter, Matthew and Granger (1921) described a new genus and species, *I. frugivorus*, based on a maxillary fragment. Simpson (1935) synonymized the genera, noting that the type and other specimens referred to *Ignacius frugivorus* were exactly like those of *Phenacolemur*, only smaller. Bown and Rose (1976) resurrected the

genus *Ignacius*, noting differences in tooth morphology and that *Ignacius* has a deeper and narrower mandible in relation to the cheek teeth. Rose and Gingerich (1976) and Rose (1981) further supported the separation of *Ignacius* and *Phenacolemur* on the basis of tooth and cranial morphology. The isolated m3 (RAM 6433) from the Goler Formation is most similar to m3s referred to *Ignacius*.

The Goler m3 is very similar to specimens referred to *Ignacius frugivorus* by Krause (1978) from the Roche Percée Local Fauna, Ravenscrag Formation, Saskatchewan, Canada. The Roche Percée specimens and RAM 6433 have small paraconids and metaconids and a notch posterior to their hypoconids (Krause, 1978:fig. 5, UA 8839) and are almost identical in size (length 2.5–2.8 mm, width 1.4–1.5 mm; Krause, 1978:table 7; RAM 6433 length 2.94 mm, width 1.47 mm). RAM 6433 is also very similar in size to AMNH 17405 (length 2.9 mm, width 1.6 mm) from Mason Pocket, Animas Formation, Colorado, which was referred to *Ignacius* ("*Phenacolemur*") *frugivorus* by Simpson (1935). Compared with other Paleocene–Early Eocene species of *Ignacius*, RAM 6433 is larger than m3s of *Ignacius fremontensis* Gazin, 1971, from the Shotgun Fauna, Fort Union Formation, Wyoming (Gazin, 1971), and much smaller than *Ignacius graybullianus* Bown and Rose, 1976, from the Willwood Formation, Wyoming (Bown and Rose, 1976:table II).

Two m3s referred to *Ignacius frugivorus* (length × width, 2.80 × 1.20 mm and 2.60 × 1.50 mm) from the Tongue River Formation of North Dakota by Holtzman (1978) are smaller than RAM 6433 (2.94 × 1.47 mm), but morphologically they are nearly identical to the Goler specimen. Especially significant is their trigonid morphology, as both RAM 6433 and SMM P77.7.131 have a small, but distinct, paraconid and metaconid, a labially deflected paraconid, and a metaconid and protoconid that are positioned subparallel to one another (Holtzman, 1978:fig. 8).

Compared with m3s of species of *Phenacolemur*, RAM 6433 is much larger than that of *Phenacolemur simonsi* Bown and Rose, 1976 (Bown and Rose, 1976:table III; Robinson and Ivy, 1994:table 4), and much smaller than those of *Phenacolemur praecox* and *Phenacolemur jepseni* Simpson, 1955 (Simpson, 1955:tables 4 and 6). *Phenacolemur pagei* Jepsen, 1930, is most similar to RAM 6433 in morphology and size, although *P. pagei* is slightly larger (Simpson, 1955:table 2). However, in his description of the dentition of *Phenacolemur*, Simpson (1955) drew heavily on the specimens of *P. pagei* from the Silver Coulee Quarry, Polecat Bench Formation, Wyoming, and noted that "the paraconid is so small and so nearly fused with the metaconid that it cannot be distinguished at all except when practically unworn" (Simpson, 1955:431). In contrast, the paraconid and metaconid on the Goler m3 would merge only after moderate to heavy wear. Finally, the talonid notch is poorly defined or absent in *Ignacius* and typically well marked in *Phenacolemur* (Rose, 1981). RAM 6433 lacks a well defined talonid notch.

Family Plesiadapidae Trouessart, 1897

Plesiadapis Gervais, 1877

Plesiadapis anceps Simpson, 1936

Plesiadapis cf. *P. anceps*

Figure 6A–E; Table 1

HOLOTYPE. AMNH 33822, left lower jaw with incisor and m1–3, right p4 and m1, right P3–M1, left M1–2, and other fragments, all from one individual. Scarritt Quarry, Fort Union Formation, early Tiffanian, Montana.

REFERRED SPECIMENS. Five m3s (RAM 6960, RAM 6963, RAM 6700, RAM 6961, RAM 6934), 1 m2 (RAM 6446), 1 mx fragment (RAM 6935), 1 mx trigonid (RAM 6946), 1 M3 (RAM 6957), 1 M2 (RAM 6962), 1 P4 (RAM 6931), and 2 I1s (RAM 6431, RAM 6929) from locality V98012. One m3 (RAM 6925) from locality V94014.

DESCRIPTION. Compared with *Paromomys* and *Ignacius*, the sample referred to *Plesiadapis* cf. *P. anceps* from the Goler Formation is relatively large, consisting of 14 complete or partial teeth whose measurements are given in Table 1 (except RAM 6946).

Incisors. Two damaged upper left incisors were recovered (Fig. 6A). Only the crown is present on RAM 6929 because the tooth is broken just above the position of the posterocone. RAM 6929 has a prominent anterocone and laterocone and a minute mediocone. The tip of the tiny mediocone is missing because of breakage. A centroconule is not present. RAM 6431 has a prominent anterocone. Both the laterocone and posterocone are broken off at their base, but both cusps were large, as shown by the size of the breaks. There is no trace of a mediocone or centroconule.

Premolars. Only a single premolar was recovered, an unworn and well-preserved P4 (RAM 6931; Fig. 6B). RAM 6931 has a very large paracone and a smaller but prominent protocone. There is no trace of a metacone. A small paraconule is closely appressed to, and positioned high on the lingual slope of, the paracone. The paraconule and protocone are subequal in height. A weakly developed paracrista extends from the paracone to the anterolabial margin of the tooth where a very small parastyle is present. A well-developed crest runs posteriorly from the paracone and terminates at a small metastyle. A cingulum is developed only on the posterior margin of RAM 6931 between the posterior slope of the protocone and the metastyle.

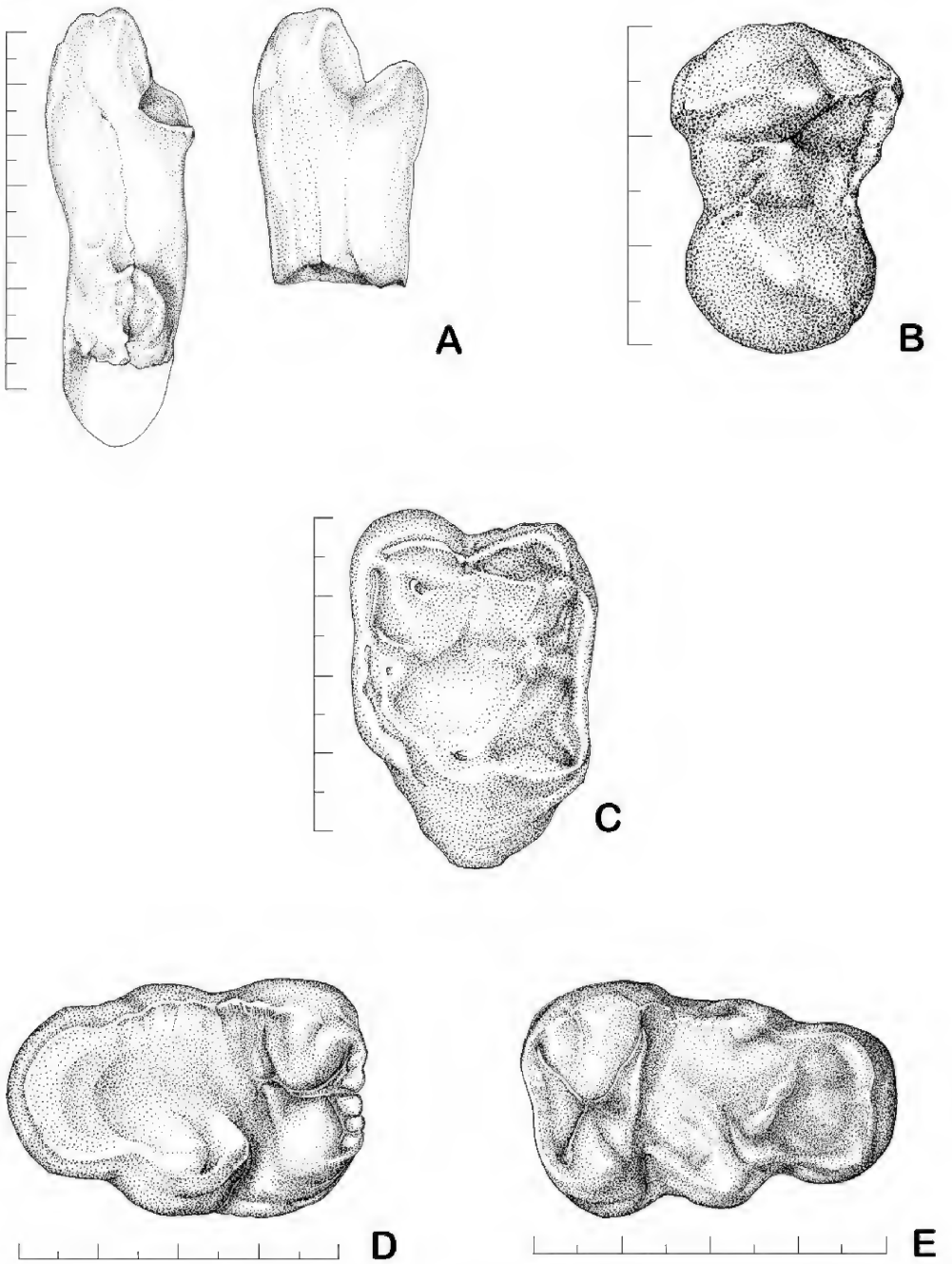

Figure 6 *Plesiadapis* cf. *P. anceps* Simpson, 1936, occlusal views of isolated teeth from locality V98012: **A,** RAM 6431 (left) and RAM 6929 (right), left I1's, scale bar = 7 mm; **B,** RAM 6931, left P4, scale bar = 3 mm; **C,** RAM 6962, left M2, scale bar = 4 mm; **D,** RAM 6700, right m3, scale bar = 4 mm; **E,** RAM 6963, left m3, scale bar = 4 mm.

Upper Molars. Two upper molars were recovered, a damaged M3 (RAM 6957), and a well-preserved M2 (RAM 6962; Fig. 6C). RAM 6957 is slightly worn and is missing its anterolabial corner (paracone is entirely absent). A small metacone is present, as are a very small paraconule and metaconule. A strongly developed preprotocrista connects the paraconule with the protocone. The protocone is large and broad, with 2 to 3 enamel crenulations developed both on its anterolingual and posterolabial slopes, with those on the latter being much better developed.

Table 1 Measurements (mm) of isolated *Plesiadapis* teeth from the Goler Formation.

Specimen no.	Tooth position	Length	Width
RAM 6963	m3	4.32	2.95
RAM 6960	m3	4.52	3.16
RAM 6700	m3	4.59	3.15
RAM 6961	m3	4.84	3.20
RAM 6934	m3	—	2.82*
RAM 6925	m3	4.79	3.38
RAM 6446	m2	3.55*	3.15*
RAM 6935	mx	—	2.75*
RAM 6931	P4	2.30	3.11
RAM 6962	M2	3.35	4.62
RAM 6957	M3	2.94*	3.61*
RAM 6929	I1	—	3.22
RAM 6431	I1	—	2.96*

RAM 6925 from V94014; all others from V98012.
* Tooth incomplete, so measurement is a minimum.

Both a precingulum and a postcingulum are present, and they terminate labially at the paraconule and metaconule, respectively. A weakly developed ridge stretches posteriorly from the protocone to the postcingulum, but a distinct hypocone is not evident.

RAM 6962 is slightly worn and its paracone and metacone are large, with the paracone being slightly broader. A strong ectoflexus is present, as are a centrocrista, paracrista, and metacrista. RAM 6962 has no trace of a metastyle, parastyle, or mesostyle. Both a small paraconule and metaconule are present, and well-developed preprotocrista and postprotocrista connect these cusps to a large and broad protocone. A small hypocone is located on a crest that runs posteriorly from the protocone and merges with the postcingulum. A well-developed cingulum rings the tooth's margin except along the lingual slope of the protocone and hypocone and at the terminus of the metacrista.

Lower Molars. These nine teeth provide the most comprehensive data for this species and six of them are complete or partial m3s that give some perspective on variation at a particular tooth site. A general description of these m3s is given on the basis of RAM 6700, a slightly worn specimen (Fig. 6D). Variations in morphology or important features are noted in the brief descriptions of the other m3s.

RAM 6700 has a small metaconid and paraconid, with the former being slightly higher and much larger. The protoconid is subequal in size to, but lower than, the metaconid. The paracristid is well developed, the protocristid much less so. The talonid is dominated by a very large, rounded hypoconulid lobe that is not fissured and has no evidence of crenulations. The hypoconid is large, and it is separated by a lingually sloping, shallow valley from a smaller and less elevated mesoconid, which is very close to the trigonid. An entocristid is well developed, but a distinct entoconid is not present. The entocristid rises in elevation from the talonid notch to merge with the hypoconulid lobe. The deep talonid basin is deepest adjacent to the talonid notch. RAM 6700 is widest at the hypoconid region of the talonid. Directly posterior to the hypoconid, the tooth's margin deflects lingually, which demarks the beginning of the hypoconulid lobe. A distinct labial cingulum is present.

RAM 6934 is very slightly worn, and only the talonid is preserved. The hypoconulid lobe is rounded, and a few shallow crenulations are developed on the posterior part of the talonid basin that impinge slightly onto the hypoconulid lobe.

RAM 6961 is moderately worn. Its hypoconulid lobe is squared and most of the enamel on the talonid is missing because of wear and breakage. If fissures were present, they have been obscured.

RAM 6960 is heavily worn and the enamel on the talonid has been breached by wear in many places. The hypoconulid lobe is rounded. An area of enamel is preserved near the rear of the talonid basin, which has a few shallow crenulations.

RAM 6925 is moderately worn and slightly damaged. A section of enamel is missing from the lingual trigonid wall. The hypoconulid lobe of RAM 6925 is rounded and has 2 small fissures that are deepest on the anterior part of the lobe. These fissures terminate before reaching the posterior margin of the lobe. The talonid of RAM 6925 is more strongly crenulated then any of the other m3s, with 4 or 5 deep crenulations developed in the posterior part of the talonid basin. These crenulations also extend onto the lingual slope of the hypoconid. Unlike other m3s, the entocristid remains elevated as it merges with the trigonid, and thus a talonid notch is not present.

RAM 6963 is unworn and well preserved (Fig. 6E). The talonid is different from the other m3s in a number of ways. The talonid basin is relatively shallow, being deepest just anterior to the hypoconulid lobe. In this same area, a few shallow crenulations are developed that extend onto the anterior part of the hypoconulid lobe. The hypoconid of RAM 6963 is similar to that of other m3s, but its mesoconid is ridgelike, lacking a distinct apex. Also, there is a distinct cusp on the entocristid, subparallel to the hypoconid. Posterior to this entocristid cusp, the tooth's margin deflects slightly labially, more so than in the other Goler m3s. Also, unlike the other m3s, there is a small cusp developed just posterior to the hypoconid. Posterior to this cusp, the tooth's margin is deflected strongly lingually. Thus, with both its labial and lingual anterior margins deflected toward the axis of the talonid basin,

the hypoconulid lobe of RAM 6963 is markedly squared in appearance.

Three other teeth are identified as lower molars; a nearly complete m2 (RAM 6446) and two broken teeth (RAM 6935 and 6946). Both RAM 6935 and RAM 6946 are too damaged to determine which tooth site they represent. RAM 6946 is a fragment of a trigonid that is missing its lingual wall, including all of the metacone. On the basis of color and wear, RAM 6946 might be the missing trigonid of RAM 6934 (m3). RAM 6935 is more complete, having preserved the entire trigonid and the anterior portion of the talonid.

RAM 6446 is a nearly complete m2 that is chipped along its entire exterior edge. Thus, much of the base of the tooth is missing, including a large part of the lingual wall of the trigonid. The paraconid and metaconid of RAM 6446 are subequal in size, with both a paracristid and protocristid present, the former being better developed. The hypoconid is much larger than the entoconid, and the entoconid corner is curved. A small labial cingulum is present.

DISCUSSION. On the basis of size and general morphology, we conclude that these 14 isolated teeth are from a single species. All but RAM 6925 are from a single locality, which lends support to the single species hypothesis. The six m3s provide information about variability at a single tooth site, and their morphology does exhibit significant variation, indicating that perhaps more than one species is present. However, without more complete material, this cannot be determined. Bearing in mind this caveat, we discuss the various genera and species of plesiadapids in relation to the Goler Formation specimens.

Five genera of plesiadapids are known from Torrejonian through Clarkforkian rocks in North America: *Pronothodectes* Gidley, 1923; *Saxonella* Russell, 1964; *Nannodectes* Gingerich, 1975; *Chiromyoides* Stehlin, 1916; and *Plesiadapis*. Specimens referred to *Saxonella* and *Pronothodectes* are much smaller than those of the Goler Formation sample listed in Table 1 (for *Pronothodectes* see Gingerich, 1976; for *Saxonella* see Fox, 1991). Also, upper central incisors of *Chiromyoides* are extraordinarily robust (Gingerich, 1976), which contrasts with the conservative morphology of the two Goler incisors.

Of the four species of *Nannodectes*, the two largest species, *Nannodectes simpsoni* Gazin, 1971, and *Nannodectes gidleyi* Matthew, 1917, are nearly equal in size to Goler specimens (Gingerich, 1976:tables A-5 and A-6). However, unlike the Goler sample, *N. gidleyi* has highly crenulated m3 talonid enamel and M2s with mesostyles (Gingerich, 1976). The m3s of *N. simpsoni* (USNM 20756, 20751) have uncrenulated talonid enamel, but they are smaller and have narrower hypoconulid lobes than the Goler Formation specimens.

With regard to European species of *Plesiadapis*, the only one that approaches the general morphology seen in the Goler sample is *Plesiadapis walbeckensis* Russell, 1964. The m3 of Walbeck specimen GH Wa 392 is similar to Goler m3s in most respects, but GH Wa 392 has a fissured heel and its number of talonid enamel crenulations exceeds anything seen in Goler m3s. Also, *P. walbeckensis* has a large mediocone on the central upper incisor (Gingerich, 1976), unlike either of the two Goler incisors.

There are many North American species of *Plesiadapis*, but most can be quickly eliminated. On the basis of size, compared with the Goler specimens, *Plesiadapis praecursor* Gingerich, 1975, is too small and *Plesiadapis simonsi* Gingerich, 1975; *Plesiadapis cookei* Jepsen, 1930; and *Plesiadapis gingerichi* Rose, 1981, are far too large. *Plesiadapis dubius* Matthew, 1915; *Plesiadapis fodinatus* Jepsen, 1930; and *Plesiadapis churchilli* are closer in size to the Goler Formation sample, but the smallest specimens of these species at each particular tooth site (Gingerich, 1976:tables A-9–A-12) exceed or equal the size of the largest tooth from the comparable tooth site in the Goler Formation sample (Table 1). Furthermore, unlike the Goler sample, *P. fodinatus*, *P. dubius*, and *P. churchilli* have strong mesostyles on upper molars and fissured heels on m3s; *P. fodinatus* and *P. dubius* have highly crenulated talonid enamel on m3s, and *P. churchilli* and *P. fodinatus* have small or well-developed centroconules on upper central incisors (Gingerich, 1976).

The Goler Formation specimens are most similar to *Plesiadapis rex* Gidley, 1923, and *Plesiadapis anceps* in size and general morphology. With regard to size, there is considerable overlap between the samples referred to *P. anceps* from the Bison Basin Saddle locality (Gingerich, 1976:table A-7) and the holotype of *P. anceps* (AMNH 33822) from Scarritt Quarry (Simpson, 1936) with that of the sample referred to *P. rex* from the Cedar Point Quarry (Gingerich, 1976:table A-8). The Goler Formation sample generally falls into this zone of overlap or it is more similar to *P. rex* (Table 1).

In his monograph on plesiadapids, Gingerich (1976) described various morphological features used to distinguish *Plesiadapis anceps* from *P. rex*, some of which are evident in the small Goler sample of isolated teeth. Key features of the Goler Formation specimens are: upper incisors lack centroconules, mediocone absent on RAM 6431 and minute on RAM 6929, the only complete upper molar (RAM 6962) lacks a mesostyle, and m3s have squared to rounded hypoconulid lobes with smooth to slightly crenulated talonid enamel. Also, hypoconulid lobe fissures are absent except on RAM 6925, whose weakly developed fissures do not divide the lobe into medial and lateral parts.

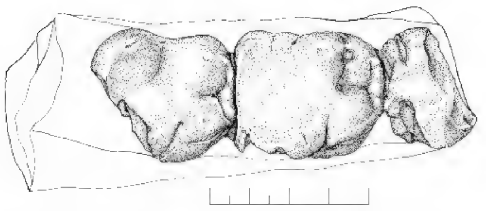

Figure 7 *Plesiadapis* cf. *P. churchilli* Gingerich, 1975, right mandible fragment with damaged p4, m1, and m2, RAM 7193 from locality V200202, occlusal view. Scale bar = 4 mm.

Plesiadapis anceps lacks an M2 mesostyle, has a small mediocone but no centroconule on the central upper incisor, and has a hypoconulid lobe that varies from squared to rounded, with smooth enamel and small fissures on half of known specimens (Gingerich, 1976). In contrast, *P. rex* usually has a mesostyle on M2, a centroconule and small mediocone on the central upper incisor, and an m3 hypoconulid lobe that tends to be broad, squared, usually with moderately crenulated enamel, and a single, small fissure that divides the lobe into medial and lateral parts (Gingerich, 1976).

In general, the Goler sample is more similar to *P. anceps* than to *P. rex*. Key features that contrast Goler specimens with *P. rex* are: lack of a mesostyle on RAM 6962 (M2), lack of a centroconule on both Goler upper incisors, and lack of a fissure on the hypoconulid lobe of m3 that divides it into two parts, and the lobe of Goler m3s tend to range between rounded and squared. Key features that contrast Goler specimens with *P. anceps* are: presence of crenulations on some hypoconulid lobes of Goler m3s, lack of a mediocone on RAM 6931, and slightly larger size of some Goler specimens. Thus, in most features, the Goler sample resembles *P. anceps*. Also, certain Goler specimens, such as RAM 6700 (m3), are almost identical to specimens of *P. anceps* from the Bison Basin Saddle locality (USNM 20587).

The Goler sample of isolated teeth is more similar to *Plesiadapis rex* in size, but it is more similar to *P. anceps* in morphology. Therefore, these teeth are designated *Plesiadapis* cf. *P. anceps*, denoting their close morphological similarity to *Plesiadapis anceps*.

Plesiadapis churchilli Gingerich, 1975

Plesiadapis cf. P. churchilli
Figure 7

HOLOTYPE. PU 21234, left mandible with i1, p3–4, and m1–3. Long Draw Quarry, Polecat Bench Formation, late Tiffanian, Wyoming.

REFERRED SPECIMEN. Partial right mandible with talonid fragment of p4, m1, and broken m2 (RAM 7193) from locality V200202.

DESCRIPTION. RAM 7193 is a fragmentary right ramus containing a damaged p4, m1, and m2. The p4 is broken anterior to the heel. The damaged heel has a shallow talonid basin with a hypoconid and broken entoconid. Both m1 and m2 are broken at the hypoconid corner. The two molars appear to be water worn, with consequent reduction of morphological detail; for example, no enamel crenulation is observable, if it were ever present. A prominent basal cingulum is present on the protoconid and continues posteriorly to the break on the hypoconid. A worn cuspule is present in the m1 talonid notch. A slight swelling is present in nearly the same position on the anterolingual margin of the entoconid of m2. The m1 entoconid corner is squared, whereas the m2 entoconid corner is curved, resulting in the anterior displacement of the entoconid. Because of breakage of the hypoconid on m1 and m2, widths of these teeth are only approximate. Measurements (in mm): p4 width, 2.68 (estimated); m1 length × width, 3.80 × 3.15 (estimated); m2 length × width, 3.80 × 3.40 (both estimated).

DISCUSSION. Compared with various species of *Plesiadapis*, RAM 7193 differs from *Plesiadapis praecursor* and *P. anceps* in its larger size (Table 2). In addition, the buccal cingula on m1 and m2 of RAM 7193 are more robust. Compared with *P. rex*, the m1–2 of RAM 7193 are longer, but of similar estimated width (Table 2), and the p4 estimated talonid width is at the upper end of the size range for *P. rex* given by Gingerich (1976). On the p4 of RAM 7193, the short talonid is transversely broader and more basined than on *P. rex* (cast of PU 20058 from Cedar Point Quarry). Although the p4 entoconid of the Goler specimen is partly broken, it appears to have been a larger, more distinct cusp than in *P. rex*. The m1 entoconid corner on RAM 7193 is squared as in *P. rex*, but the m2 entoconid corner is more curved. The m1–2 labial cingula are more robust than on *P. rex*.

The Goler Formation specimen is similar in size to specimens of *Plesiadapis churchilli*. Compared with the sample from Long Draw Quarry (Gingerich, 1976), RAM 7193 differs in having a longer m1 (Table 2). Compared with Winterfeld's (1982) sample of *Plesiadapis* sp., probably *P. churchilli* from the Rock Springs Uplift, RAM 7193 also has a slightly longer m1 and a wider p4 talonid. However, all measurements for the Goler specimen fall within the ranges given by Krause (1978) for the *P. churchilli* sample from the Roche Percée Local Fauna. The p4 talonid on RAM 7193 is weakly basined and transversely broader than that of *P. churchilli* (PU 21235 type), in which the talonid is domed, and the entoconid of RAM 7193 is more distinct than on *P. churchilli*. The m1 entoconid corner is squared in both RAM 7193 and *P. churchilli*, and the m2 entoconid corner is rounded on RAM 7193 and

Table 2 Measurements (mm) of *Plesiadapis* m1s from North America compared with RAM 7193 from the Goler Formation in Primate Gulch (locality V200202).

Plesiadapis species	Locality and age	Length	Width	Number
praecursor	Douglas Quarry/Keefer Hill: Ti1	2.6–2.7	2.5–2.7	5
anceps	Bison Basin Saddle: Ti2	2.6–3.0	2.7–3.0	11
rex	Cedar Point Quarry: Ti3	2.7–3.4	2.6–3.4	126
Churchill	Long Draw Quarry: Ti4	3.4–3.6	3.2–3.5	4
cf. *churchilli*	Primate Gulch: Ti4?	3.80	3.15*	1
fodinatus	Princeton Quarry: Ti5	2.8–3.5	2.7–3.2	34
simonsi	Midlevel Sand Draw: Ti5	3.9–4.0*	3.9*	2
gingerichi	Clark's Fork Basin: Ti6-Cf1	4.5–4.75	3.9–4.4	3
cookie	Little Sand Coulee area: Cf1	5.1–5.7	4.8–5.4	7
dubius	Paint Creek: Cf2	2.7–3.1	2.5–2.7	3

Measurements of *P. gingerichi* from Rose (1981); all others, except RAM 7193, from Gingerich (1976).
* Estimated.

some specimens of *P. churchilli*, including the holotype. A prominent buccal cingulum is present on the molars of some specimens in Winterfeld's (1982) sample. RAM 7193 resembles *P. churchilli* from Roche Percée in having the small cuspule at the base of the talonid notch on m1. This cuspule fills the talonid notch, whereas it appears to be a little smaller in the Roche Percée specimens illustrated by Krause (1978). A tiny cuspule appears also to be present in the m2 talonid notch of *P. churchilli* from Roche Percée. On the m2 of RAM 7193, the talonid notch is reduced to a narrow crease, and only the aforementioned slight swelling is present.

RAM 7193 is also similar in size to *Plesiadapis fodinatus*, differing by having a greater m1 length (Table 2). The p4 of RAM 7193 resembles that of *P. fodinatus* (cast of PU 13930) in having a short, weakly basined talonid (in contrast to *P. churchilli*), with a distinct entoconid cusp present; this cusp, absent in *P. churchilli*, is said to be present on most specimens of *P. fodinatus* (Gingerich, 1976). *Plesiadapis fodinatus* differs from the Goler specimen in having noticeably curved entoconid corners on both m1 and m2, whereas the m1 entoconid corner of RAM 7193 is squared and the m2 corner is less curved (comparison made with PU 13930). Because the m1 posterolingual corner in *P. fodinatus* is curved, with the entoconid anteriorly displaced, the talonid notch is distinctly narrower than on RAM 7193. The m2 notch is also slightly narrower on *P. fodinatus* because of the greater anterior displacement of the entoconid. The curved, rather than squared, entoconid corners of m1–2 are features associated with later species of *Plesiadapis* (Gingerich, 1976). *Plesiadapis fodinatus* also is characterized by having more crenellated enamel than *P. churchilli*; no distinct crenellation is observable on the Goler specimen, but some morphological detail has probably been lost because of wear.

RAM 7193 differs from *Plesiadapis simonsi* in having a squared entoconid corner on m1, whereas in *P. simonsi*, the m1 posterolingual corner is strongly curved, with the entoconid displaced anteriorly. The m1–2 lengths of RAM 7193 and PU 17814 (holotype of *P. simonsi*) are similar (Table 2), but the trigonid widths are greater in *P. simonsi* (because of breakage, the talonid widths on RAM 7193 cannot be obtained).

Plesiadapis dubius differs from RAM 7193 in being much smaller (Table 2) and having curved entoconid corners on both m1 and m2. *Plesiadapis gingerichi*, *P. cookei*, and the European *Plesiadapis tricuspidens* Gervais, 1877, are much larger than RAM 7193 (Table 2), with the latter two species having curved, crested entoconids on the m1 (in addition to m2). The European species *Plesiadapis insignis* Piton, 1940, and *Plesiadapis walbeckensis* are much smaller than RAM 7193; in addition, the heel on the p4 of *P. walbeckensis* is unbasined and without a distinct entoconid. The European *Plesiadapis remensis* Lemoine, 1887, is similar in size to RAM 7193, but it has been reported to have curved entoconid crests on both m1 and m2 and an unbasined p4 heel (Gingerich, 1976). Also, RAM 7193 is much larger than the largest species of *Nannodectes*, *N. gidleyi*.

The size and morphological similarities that RAM 7193 shows with teeth of *Plesiadapis churchilli* and *P. fodinatus* make it unlikely that this specimen belongs to a genus other than *Plesiadapis*. Based on the comparisons made above, RAM 7193 is most similar to *P. churchilli*, with fewer similarities to *P. fodinatus*. The Goler Formation specimen is closest in size to *P. churchilli*, and it resembles that species in retaining a squared entoconid corner on the m1. The molar entoconid corners of *P. fodinatus* are noticeably more curved than on RAM 7193. Also, absence of enamel crenulation on the molars suggests that, although the molars are water worn, intense enamel crenulation as found in *P. fodinatus* might never have been present. Thus, the overall molar morphology of RAM 7193 more closely resembles that of *P. churchilli*

than that of *P. fodinatus*. However, the p4 of RAM 7193 is advanced and resembles that of *P. fodinatus* in having a short, weakly basined talonid with a distinct entoconid, features absent in *P. churchilli*. These two species are closely related, and Gingerich (1976) suggested that *P. fodinatus* evolved from *P. churchilli*. Thus, it is not unexpected to find a specimen showing features of both named species.

MAMMALIAN BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Until the 1990s, the age of the Goler Formation was a matter of considerable uncertainty, as few fossils were available. Based on admittedly sparse data, McKenna (1960) and McKenna et al. (1987) argued that the only major mammal-yielding locality, the Laudate Discovery Site, was probably late Torrejonian or early Tiffanian in age. The late Paleocene or early Eocene invertebrates in Member 4d (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; Squires et al., 1988; Reid and Cox, 1989) helped constrain the age of strata near the top of the formation, but they were of little utility in constraining the age of the subdivisions below.

Recent efforts have yielded new mammal sites both higher and lower in the formation than the Laudate Discovery Site (Fig. 2), and more fossils are now available primarily because of the success of screen-wash sampling. On the basis of structural orientation of the formation, where beds dip generally north, the highest locality, Honey Pot, is approximately 590 m above the Member 4a–4b contact, and the lowest, Land of Oz, is approximately 300 m below the same contact. These two sites have not, as yet, yielded primates. However, *Plesiadapis* has been recovered from the Laudate Discovery Site (lowermost part of Member 4b), as well as Primate Gulch and the Edentulous Jaw Site (both in the lower part of Member 4b). *Plesiadapis* is not known from rocks older than Tiffanian (Archibald et al., 1987; Lofgren et al., 2004a), indicating that the lower part of Member 4b is Tiffanian in age or younger.

Gingerich (1976) proposed a lineage zone subdivision of the Tiffanian on the basis of nonoverlapping species of *Plesiadapis* (Fig. 8). As discussed earlier, the species from the Laudate Discovery Site and the Edentulous Jaw Site, referred to *Plesiadapis* cf. *P. anceps*, is more similar to *P. rex* in size but more similar to *P. anceps* in morphology. On the basis of Gingerich's (1976) zonation, the presence of *P. anceps* denotes Tiffanian (Ti) lineage zone Ti2, and the presence of *P. rex* denotes Tiffanian lineage zone Ti3. If this zonation can be extended to California, the two sites, and thus the lower part of Member 4b, is roughly correlative to lineage zone Ti2, or perhaps Ti3 (Fig. 8). Similarly, Primate Gulch yielded a single jaw fragment referred to *Plesiadapis* cf. *P. churchilli*, and on the basis of Gingerich's (1976) zonation, Primate Gulch would correlate approximately to Tiffanian lineage zone Ti4 (Fig. 8).

It is important to note that stratigraphic relationships between the three sites yielding *Plesiadapis* are very uncertain. The Goler Formation can be well exposed locally, but most of the formation is covered. Because the Laudate Discovery Site and Edentulous Jaw Site are separated by over 2 km of mostly covered exposures, physical correlation of the sites is not possible. Primate Gulch is only 0.3 km north of the Edentulous Jaw Site, and it appears to be stratigraphically higher on the basis of the general structural trend of the formation where beds usually dip north. But physical correlation of Primate Gulch and the Edentulous Jaw Site is not possible, because intervening outcrops are covered, local outcrops show evidence of folds, and Cox (1982) mapped a geological fault between the sites. Consequently, interpretations of the relative ages of the Laudate Discovery Site, Edentulous Jaw Site, and Primate Gulch are based almost solely on fossils.

The presence of *Paromomys depressidens* at the Laudate Discovery Site and *Ignacius frugivorus* at the Edentulous Jaw Site provide both supporting and conflicting data compared with correlations based on species of *Plesiadapis*. *Paromomys* is relatively common in Torrejonian assemblages, but rare in Tiffanian ones. The youngest records of the genus are specimens referred to *Paromomys* cf. *P. depressidens* from the Cochrane 2 site (Porcupine Hills Formation) in Alberta, Canada (Krause, 1978), and the Shotgun Fauna (Keefer Hill) (Fort Union Formation) in Wyoming (Gazin, 1971). Both sites are interpreted to be earliest Tiffanian (Ti1) (Archibald et al., 1987; Lofgren et al., 2004a). If the Laudate Discovery Site is indeed Ti2–Ti3, then the Goler Formation occurrence would be the youngest known for *Paromomys*. Conversely, but less likely, the Laudate Discovery Site could be Ti1.

In contrast, *Ignacius frugivorus* is known from sites that are similar in age (on the basis of *Plesiadapis* zonation) to the Edentulous Jaw Site (Ti2–Ti3). For example, Cedar Point Quarry (Rose, 1981), Scarritt Quarry (Rose, 1981), and Brisbane (Holtzman, 1978) are either Ti2 or Ti3 (Archibald et al., 1987; Lofgren et al., 2004a). Therefore, the Goler Formation occurrence, interpreted to be Ti2–Ti3, is consistent with the age of other sites yielding *I. frugivorus*.

The Goler Formation primates are generally similar to those from early-middle Tiffanian rocks in the Rocky Mountain States, with the exception of *Paromomys depressidens*, whose Goler occurrence appears to be a temporal vestige.

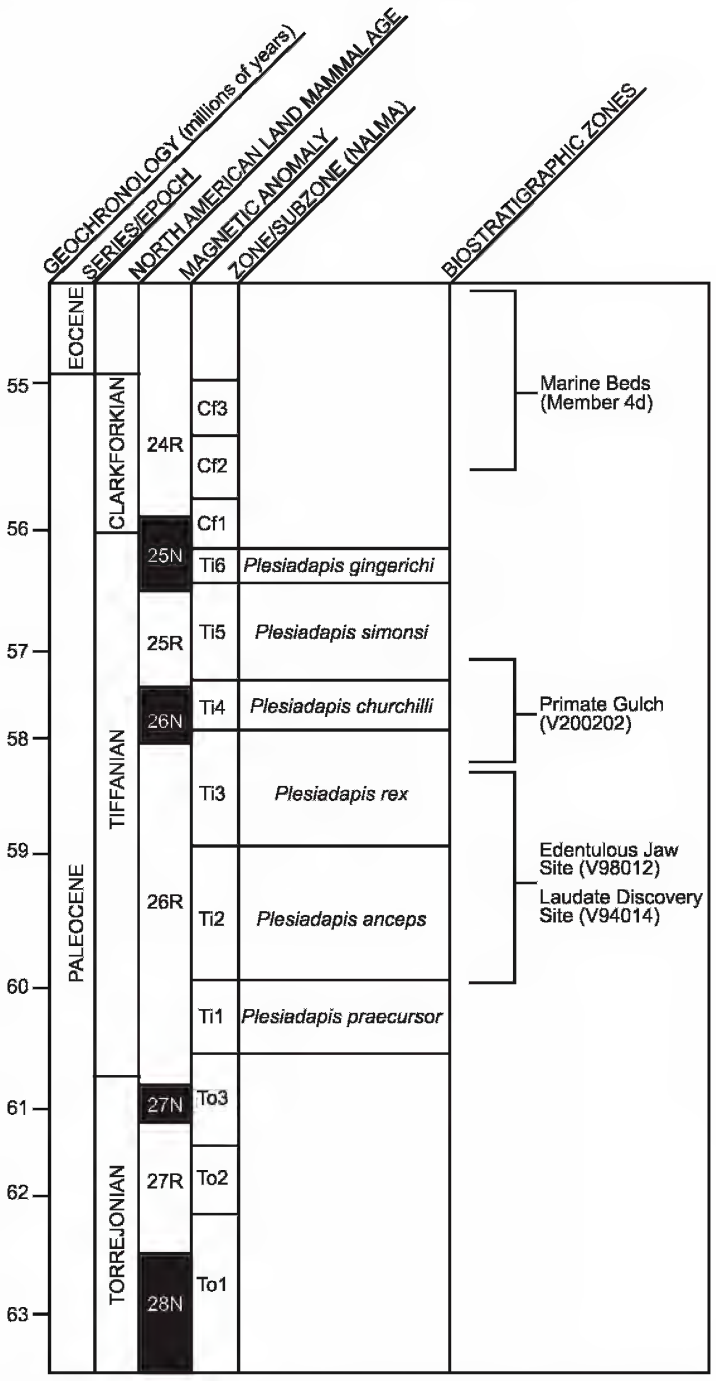

Figure 8 Correlation of the three primate-yielding sites from the Goler Formation to the Tiffanian North American Land Mammal Age. Tiffanian subdivisions are lineage zones of Gingerich (1976) based on nonoverlapping species of *Plesiadapis*. Correlation of Member 4d marine beds is also shown on the basis of invertebrate fossils (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; and Reid and Cox, 1989). Adapted from Lofgren et al. (2004a).

PALEOECOLOGY AND PALEOBIOGEOGRAPHY

Before the 1980s, the Goler Formation was thought to be entirely nonmarine. More recently, marine sediments were identified that indicated that the Goler Basin was inundated by a marine transgression in the late Paleocene or early Eocene (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; Squires et al., 1988; Reid and Cox, 1989). The marine sediments near the top of the formation in Member 4d (Fig. 2) yielded invertebrate fossils, including foraminifera. Paleoecological interpretations based on Goler foraminiferal assemblages indicate a maximum water depth of up to, or exceeding, 150 m (McDougall, 1987). Recently, shark teeth (*Striatolamia* Gluckman, 1964) were recovered from Member 4d (Lofgren et al., 2004b). The marine invertebrates from Member 4d and other fossils noted below from Members 3 and 4 indicate that, before the marine transgression, the Goler Basin was probably in close proximity to the Pacific Ocean throughout much of its history.

A single ray tooth (RAM 7180)—suborder Batoidea, family Dasyatidae, cf. *Hypolophodon* (Lofgren et al., 2002)—was recovered from the Edentulous Jaw Site (Member 4b). Batoids are characteristically nearshore marine fishes that are quite tolerant of brackish water and are often found in rivers (Bryant, 1989). Also, the species represented by a large section of turtle shell found at UCMP locality V81035 (Member 4a) is thought to be related to sea turtles (McKenna et al., 1987). Finally, a concretion from UCMP locality V5250 (Member 3) contains a bass-shaped osteichthyan fish whose fin morphology resembles beryciform fish (McKenna et al., 1987). Extant beryciforms are marine (Zehren, 1979). Cumulatively, these fossils suggest a marine influence as Goler sediments accumulated.

The depositional setting of the Goler Formation indicates that the Goler Basin was a suitable environment for aquatic vertebrates. The formation consists of 1) a lower sequence of mostly alluvial fan and braided stream deposits (Members 1–3) whose detritus was derived from nearby sources, primarily to the north, and 2) an upper sequence of braided and meandering stream deposits (Member 4, except for marine beds) containing sediment derived from more distant sources to the east (Cox, 1982). The westward-flowing river system represented by Member 4 probably emptied into the Pacific Ocean not far west of the Goler Basin. In contrast to the rarity of most other types of vertebrates in the Goler Formation, Member 4 has a relatively diverse assemblage of turtles (McKenna et al., 1987; Lofgren et al., 2002). Also, crocodilian teeth and scutes have been recovered from the Edentulous Jaw Site and Laudate Discovery Site, the two screen-wash samples from the Goler Formation. This is to be expected because turtles and crocodilians are common in Paleocene nonmarine rocks from the Rocky Mountain states. However, what is unusual is the paucity of teeth and scales of fish in Goler screen-wash samples. For example, gar scales are often very common in Paleocene fluvial deposits from elsewhere in North America, but they have not been recovered from the Goler Formation. Whether the paucity of fish remains has some ecological significance is a question that can be addressed through further sampling.

Fully terrestrial vertebrates in the Goler Formation are represented thus far only by mammals and lizards. At least three genera of lizards are present (Lofgren et al., 2002), and lizard scutes are the most common fossils in screen-wash samples (about 200 specimens). The Goler mammalian fauna is relatively diverse and contains arctocyonid, hyopsodontid, phenacodontid, and periptychid ungulates; multituberculates; marsupials; carnivores; mesonychids; and plesiadapid and paromomyid primates (Lofgren et al., 2002).

The Goler Formation primates, represented by the paromomyids, *Paromomys* and *Ignacius*, and the plesiadapid, *Plesiadapis*, were probably both terrestrial and arboreal in habit. On the basis of limb proportions, forelimb resemblances to the extant rodent *Marmota* Blumenbach, 1779, and other evidence, *Plesiadapis* is interpreted to have been primarily terrestrial (see discussion in Gingerich, 1976). In contrast, the osteology of the manus and pes of paromomyids indicates that they might have been gliders (Beard 1990, 1993). The Goler Basin would have provided ample habitat for gliders, as the presence of numerous trees is indicated by an abundance of fossil wood in Member 4. Large logs, up to a few meters in length, are commonly present in outcrops of thick, cross-bedded conglomeratic sandstone. Fossil wood is less abundant in Member 3, but pieces more than 20 cm in length are not uncommon (in contrast, sites that yield well-preserved fossil leaves or pollen are rare). Thus, coursed by meandering and braided streams that were probably lined with thick stands of vegetation, the Goler Basin provided a suitable habitat for a diverse assemblage of vertebrates, including arboreal primates.

Given that the Goler Formation now lies hundreds of miles west of other similarly aged Paleocene sites that yield plesiadapid primates (Fig. 3), Goler Formation vertebrate assemblages provide important information concerning western North American paleobiogeography. Goler vertebrate assemblages are generally similar to those from early-middle Tiffanian rocks in the Rocky Mountain states (Lofgren et al., 2002).

Therefore, considerable interchange of taxa occurred between these areas and probably no major dispersal barriers were in place. This is especially evident with regard to the arboreal Goler Formation primates, as *Paromomys depressidens* is also known from Wyoming to Alberta, and *Ignacius frugivorus* from Texas to Saskatchewan.

Conversely, even at this early stage of analysis of Goler Formation vertebrate assemblages, there is a significant indication of endemism as well. Goler Formation taxa, such as the plesiadapids referred to *Plesiadapis* cf. *P. anceps* and *P.* cf. *P. churchilli*, two new mammal taxa (arctocyonid *Mimotricentes tedfordi*, McKenna and Lofgren, 2003; periptychid *Goleroconus alfi* gen. and sp. nov., McKenna et al., 2008), and new species of turtles represented by two recently collected skulls (Lofgren et al., 2002), indicate that there was a notable degree of geographic and/or latitudinal difference between coastal California and other early-middle Tiffanian sites from western North America.

CONCLUSIONS

1. Before 1990, the Goler Formation had yielded only a few vertebrate fossils. Recent collecting efforts, using screen-washing techniques, provide a much larger sample of vertebrates, including new records of turtles, rays, lizards, crocodilians, and mammals.

   With its emerging diverse assemblage of continental vertebrates, the Goler Formation provides a unique opportunity for study of the Paleocene vertebrate fauna from the west coast of North America.
2. New records of Goler Formation mammals include three genera of primates (*Paromomys*, *Ignacius*, and *Plesiadapis*), the oldest known from California. These specimens are referred to *Paromomys depressidens*, *Ignacius frugivorus*, *Plesiadapis* cf. *P. anceps*, and *Plesiadapis* cf. *P. churchilli*.
3. The presence of *Plesiadapis* indicates that the lower part of Member 4b of the Goler Formation is Tiffanian. More specifically, the occurrence of *Plesiadapis* cf. *P. anceps* at the Laudate Discovery Site and Edentulous Jaw Site and *Plesiadapis* cf. *P. churchilli* at Primate Gulch indicates an approximate age of Ti2–Ti3 for the Laudate Discovery Site and Edentulous Jaw Site and Ti4 for Primate Gulch.
4. The occurrence of *Ignacius frugivorus* at the Edentulous Jaw Site is consistent with Ti2–Ti3, but the presence of *Paromomys depressidens* at the Laudate Discovery Site suggests either an older age or that the Goler occurrence is the youngest known for the genus.
5. Exposures of the Goler Formation are entirely nonmarine except for Member 4d, which contains late Paleocene or early Eocene marine invertebrates. A few fossils from Members 3 and 4a–b indicate a possible marine influence on the Goler Basin. These data suggest that the Goler Basin was in close proximity to the Pacific Ocean throughout much of its existence.
6. The part of the Goler Formation that has yielded vertebrate fossils (Members 3–4) was deposited primarily by braided and meandering streams. Member 4 contains a relatively diverse assemblage of vertebrates, with the remains of turtles, mammals, and lizards being somewhat common, but those of crocodilians and, particularly fish, much less so. The absence of gars is puzzling as their fossils are usually common in Paleocene nonmarine basins elsewhere in North America.
7. Goler Formation paromomyids (*Paromomys* and *Ignacius*) and plesiadapids probably lived within stands of trees that lined large streams, an interpretation supported by the abundance of fossil wood in Member 4.
8. Goler Formation vertebrate assemblages provide important information concerning North American paleobiogeography. Goler Formation vertebrates, especially the mammals, are generally similar to those from early-middle Tiffanian rocks in the Rocky Mountain states, and some taxa must have been able to move freely between the areas. However, there is also evidence of significant endemism on the basis of Goler *Plesiadapis* specimens that cannot be confidently referred to existing species, as well as new species of turtles and mammals.

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Goleroconus alfi, a new small periptychid (Mammalia, Eparctocyona) from the late Paleocene of California

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ABSTRACT. A small fossil periptychid (Mammalia, Ungulata, Eparctocyona) has been known for approximately a half century from the Paleocene-age Goler Formation of the southwesternmost Great Basin, California. In earlier work, this animal was described on the basis of frustratingly incomplete material. For reasons of nomenclatural stability, the animal has not previously been named formally. An adequate holotype has now been found, and a name is supplied here. Lack of referred upper teeth hampers detailed assessment of the animal's affinities. Nonetheless, it is determinable as a relict taxon occurring in Tiffanian rocks and related to Puercan and Torrejonian taxa that occur elsewhere.

INTRODUCTION

This paper is one of a series of studies of the geology and fossil vertebrates of the northern end of the El Paso Mountains, in the southwest corner of what is now the Great Basin, in Kern County, Southern California. Lying stratigraphically immediately beneath Miocene and younger rocks (Merriam, 1919; Whistler, 1987; Loomis and Burbank, 1988), which are well known near Red Rock Canyon along State Highway 14 (formerly Highway 6), is an older sequence of conglomeratic and feldspathic strata that are named the Goler Formation (Fig. 1, and see Dibblee, 1952; Cox and Diggles, 1986; Cox, 1987). The Goler Formation is sparingly fossiliferous. Until recently, little reliable evidence for the age of the Goler Formation had been found, but diligent prospecting over the past 50 years has produced a few specimens in its upper sediments. Currently, much additional information is accumulating at the Raymond M. Alf Museum of Paleontology (RAM) of The Webb Schools as the result of systematic prospecting, screening, and examination of concretions at a number of stratigraphic levels within the more than 3-km-thick succession of rapidly deposited Goler Formation sediments. Stratigraphic subdivisions of the Goler Formation and major vertebrate-yielding sites discussed in this paper are shown in Figure 2.

In earlier literature, the Goler Formation was often confused with various mid-Tertiary rock units, but clearly it is mostly or entirely Paleocene in age. Goler strata thus hold the key to an understanding of earlier Tertiary events, most of which occurred in the late Paleocene. Here we diagnose and describe a new periptychid from the Goler Formation and point out its relictual occurrence in rocks of Tiffanian (late Paleocene) age. Specimens referred to the same taxon are separated by as much as 585 m of section (assuming insignificant repetition of beds by faulting) and thus corroborate other evidence for the rapid deposition of at least the top part of the Goler Formation.

Paleocene mammals in the southwestern corner of the Great Basin in California were first reported more than 50 years ago (McKenna, 1955). The first specimen to be described was a fragmentary lower jaw of a small periptychid from the Laudate Discovery Site, UCMP (Museum of Paleontology, University of California, Berkeley) locality V5252 (= RAM locality V94014), stratigraphically high in the Goler Formation (Fig. 2) (Dibblee, 1967; Cox, 1987). Additional specimens of lower teeth from the same locality, evidently all belonging to the same undescribed species, have been reported by McKenna et al. (1987), and two more lower teeth apparently referable to that taxon are reported here. However, no specimen from the Laudate Discovery Site is adequate to serve as a type specimen, and no upper teeth have been identified.

Recently, a lower jaw, bearing p4, m1, m2, and part of m3, was found at a new locality (RAM locality V200120, Honey Pot) high in Member 4b of Cox (1982) of the Goler Formation, approx-

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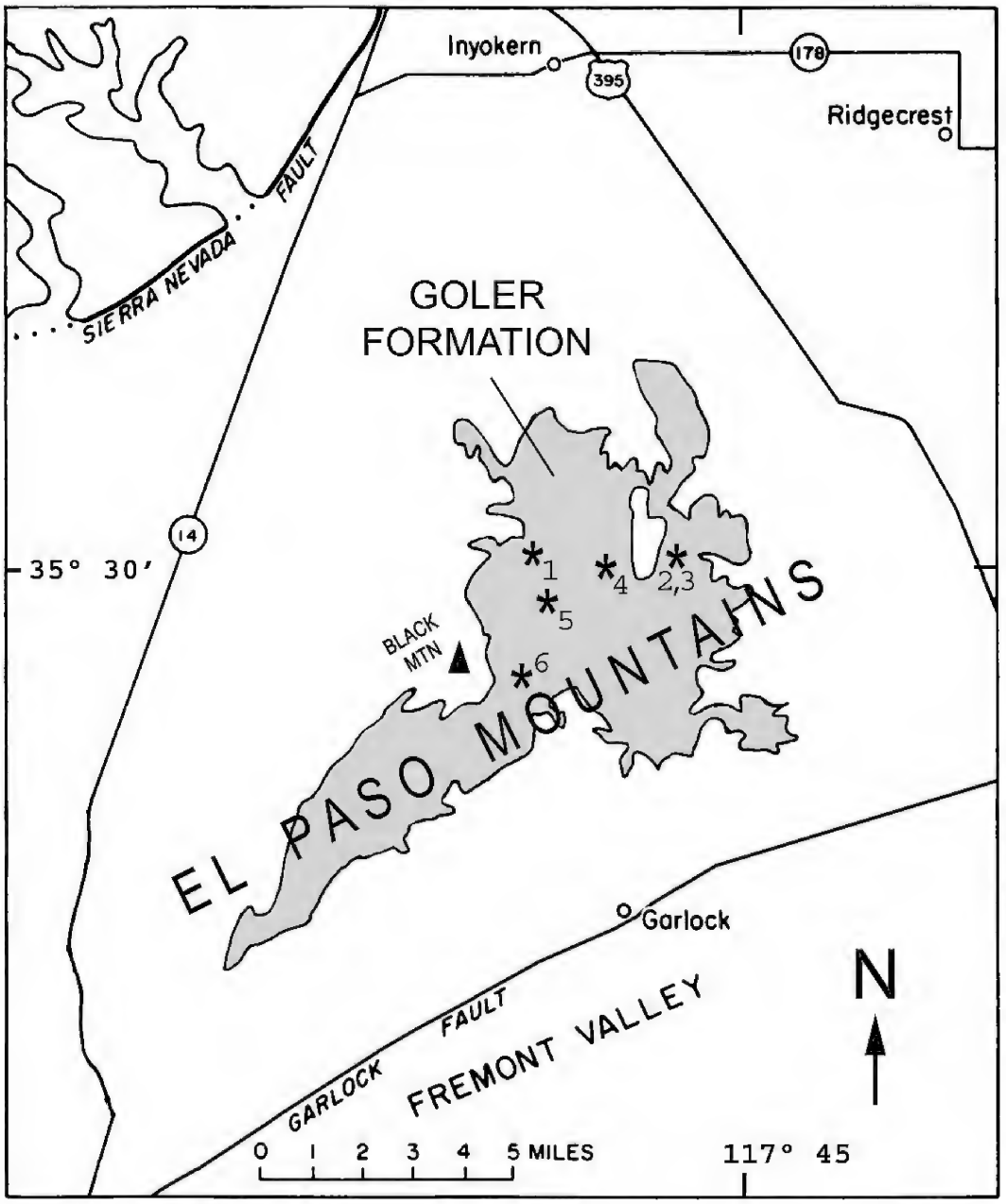

Figure 1 Outcrop map of Goler Formation (shaded) with major vertebrate sites numbered (see Figure 2 for site names; map adapted from Cox, 1987).

imately 585 m higher in the section than the Laudate Discovery Site (Fig. 2). The molars of the newly discovered lower jaw are nearly identical to isolated lower molars from the Laudate Discovery Site, suggesting that a single species is represented in the Goler Formation throughout a segment of Tiffanian (late Paleocene) time from about Ti2 through at least Ti4 (on the basis of the occurrences of two species of *Plesiadapis* Gervais, 1877, and other primates at RAM localities V200202, V98012, V94014; Fig. 2) (Lofgren et al., 2008). Therefore, we name a new periptychid genus and species on the basis of the late Tiffanian jaw, and we tentatively refer the somewhat older Laudate Discovery Site specimens to it. We supplement description of the new

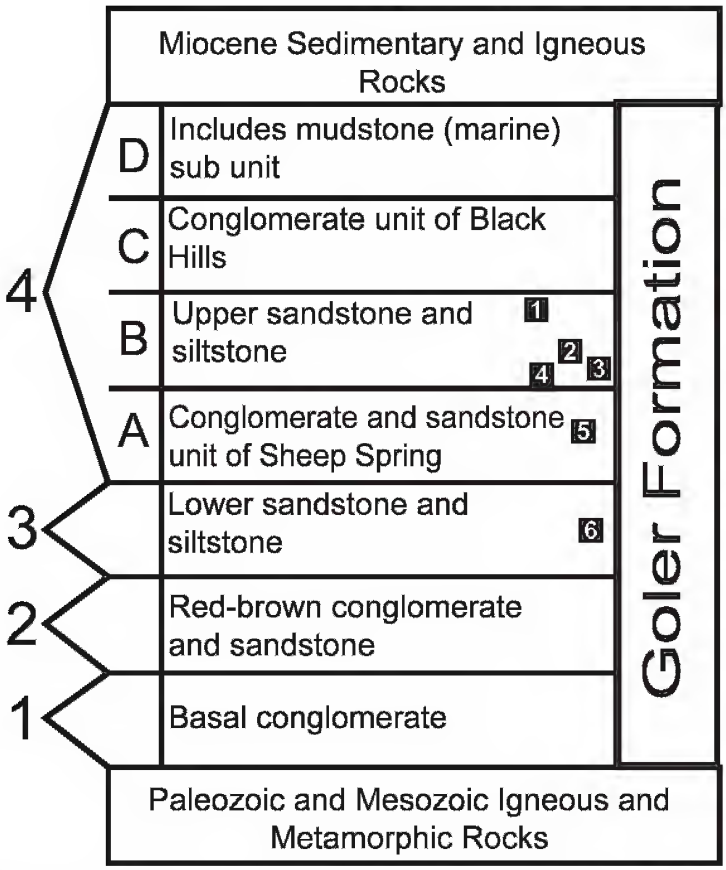

Figure 2 Diagrammatic stratigraphic subdivision of the Goler Formation, showing the four members and subdivisions of Member 4 (modified after Cox, 1987), with approximate stratigraphic position of major vertebrate-yielding sites numbered as: **1**, Honey Pot, RAM locality V200120; **2**, Primate Gulch, RAM locality V200202; **3**, Edentulous Jaw Site, RAM locality V98012; **4**, Laudate Discovery Site, RAM locality V94014; **5**, Land of Oz, RAM locality V20001; **6**, Tedford–Shultz Site. The different stratigraphic subdivisions are not to scale. Thicknesses for the Goler Formation and its subdivisions can be found in Cox (1982, 1987) and Cox and Diggles (1986). *Goleroconus* has been found in sites 1 and 4.

genus and species with additional information, notably from an isolated p3 also from the Laudate Discovery Site.

The new, small periptychid obviously represents a relictual lineage because it is not known from Paleocene rocks of the Rocky Mountain states, Texas, Mexico, or Canada. In early discussions of the age of the Goler Formation, the relictual status of this periptychid was unrecognized, and the age of the Goler Formation at and below the level of the Laudate Discovery Site was thought to be Puercan or Torrejonian (McKenna, 1960; McKenna et al., 1987). Our current understanding of the age of various fossiliferous levels of the Goler Formation is based on other taxa that have Tiffanian first appearances elsewhere (Lofgren et al., 1999, 2002). Relictual Torrejonian taxa occurring in Tiffanian strata (as defined by the presence of *Plesiadapis*) have also been documented in the Hanna Basin of Wyoming (Higgins, 2003).

ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York USA
RAM	Raymond M. Alf Museum of Paleontology, The Webb Schools, Claremont, California USA
Ti1, Ti2, etc.	Sequential divisions of the Tiffanian Land Mammal Age and rocks deposited during those times
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
UNM	Department of Geology, University of New Mexico, Albuquerque, New Mexico USA

SYSTEMATIC PALEONTOLOGY

Grandorder Ungulata Linnaeus, 1766

Mirorder Eparctocyona McKenna, 1975

Family Periptychidae Cope, 1882b

Goleroconus new genus

cf. *Conacodon entoconus* Cope, 1882a (McKenna, 1955:514).

Unnamed genus and species [of anisonchine periptychids] (McKenna, 1960:12).

Unnamed genus and species [of conacodontine periptychids] (McKenna et al., 1987:36).

Periptychid mammal (Lofgren et al., 2008).

DIAGNOSIS OF GENUS. As for the type species.

TYPE AND ONLY KNOWN SPECIES. *Goleroconus alfi* sp. nov.

ETYMOLOGY. Goler, in reference to the Goler Formation, and *conus*, Latin for cone, in reference to the inflated teeth of this genus.

RANGE. Tiffanian late Paleocene of southern California (see below).

Goleroconus alfi new species

Figures 3–6; Table 1

DIAGNOSIS OF SPECIES. Lower fourth premolar larger than molars and lingually hypsodont; p4 lacking both anterior basal cusp and labial heel cusp but having worn metaconid-like ridge and lingually crested heel; all lower molars lingually hypsodont; paraconid retained on all lower molars (including the m3 of the original jaw), although paraconid small, and when worn, resembling short, anteriorly projecting paralophid of *Haploconus angustus* Cope 1881 (AMNH 3447) and *Haploconus corniculatus* Cope, 1888, (AMNH 3538, 16693); size 157% that of *Conacodon kohlbergeri* Archibald et al., 1983b (see measurements in Table 1). *Goleroconus* is distinguished from various other periptychids by combination of features, including hypsodonty, premolar morphology, molar paraconid size and placement, position of molar talonid cusps relative to each other, and relative development of cingulids.

HOLOTYPE. RAM 7171, broken right dentary bearing p4, m1, m2, and part of the trigonid of m3, collected by J.G. Honey, May 2001.

ETYMOLOGY. The species name, *alfi*, is in honor of the late Raymond M. Alf, teacher and vertebrate paleontologist at The Webb Schools, Claremont, California, and founder of the Raymond M. Alf Museum of Paleontology.

TYPE LOCALITY. RAM locality V200120 (Honey Pot), on a talus slope, found in part of a concretion, the other parts of which have not been located despite intensive search. The specimen could have eroded from sediments that are stratigraphically higher in Member 4b, but probably not from more than 10 m stratigraphically above the level at which the specimen was found.

STRATIGRAPHIC RANGE. From near base of Member 4b of Cox (1982), upward to near top of that member of the Goler Formation of Dibblee (1952). This interval would represent about 660 m of the stratigraphic section that was presented by Cox (1987:fig. 3), and 585 m as projected by one of us (J.G.H.). The Goler Formation has been divided into informal members in four different schemes (Dibblee, 1952, 1954; Cox, 1982; Cox and Diggles, 1986; Cox, 1987; McKenna and Lofgren, 2003). In the stratigraphic terms of Cox (1987), the Laudate Discovery Site occurs near the base of Member 4b (formerly Tgsu). Rocks yielding the Laudate Discovery Site (RAM locality V94014) lie about two thirds of the way up-section from the base of the Goler Formation (Fig. 2). Strata at this level have been reported to be either late Torrejonian or early Tiffanian in age (McKenna et al., 1987). However, the level now appears to be Tiffanian on the basis of *Plesiadapis* and other primates that have been more recently recovered from the Laudate Discovery Site and RAM localities V98012 and V200202 (Lofgren et al., 1999, 2002, 2008); RAM localities V98012 and V200202 are higher in the section than RAM V94014 but still beneath the level of RAM V200120 where the holotype of *G. alfi* was found (Fig. 2). Recently collected specimens referable to *Phenacodus* sp. Cope, 1873, have been found lower in the section at RAM locality V20001, within Member 4a (Fig. 2). Thus, the mammalian assemblage from the Laudate Discovery Site now indicates a Tiffanian age, as do localities with Tiffanian fossils that bracket the site in this part of the Goler Formation. Also, the Laudate Discovery Site lies stratigraphically below strata in Member 4d that have been dated by marine fossils as either latest Paleocene or early Eocene (McDougall, 1987; Squires et al., 1988).

ASSOCIATED TAXA. There are no other vertebrate fossils at the type locality, but at lower stratigraphic levels represented by RAM localities V94014 and V98012 (Fig. 2), specimens referable to species of *Plesiadapis* and *Phenacodus* occur, suggesting Tiffanian rather than earlier age. The large multituberculate from UCMP locality V5870 (at the same stratigraphic level as RAM locality V94014 = UCMP locality 5252), which was identified as cf. *Neoliotomus* sp. Jepsen, 1930, by McKenna (1960), was later dubbed *Neoliotomus*, cf. *N. conventus* Jepsen, 1930, by R.E. Sloan (West, 1970:854–855). Elsewhere, *N. conventus* is of late Tiffanian and Clarkforkian age (Krause, 1982).

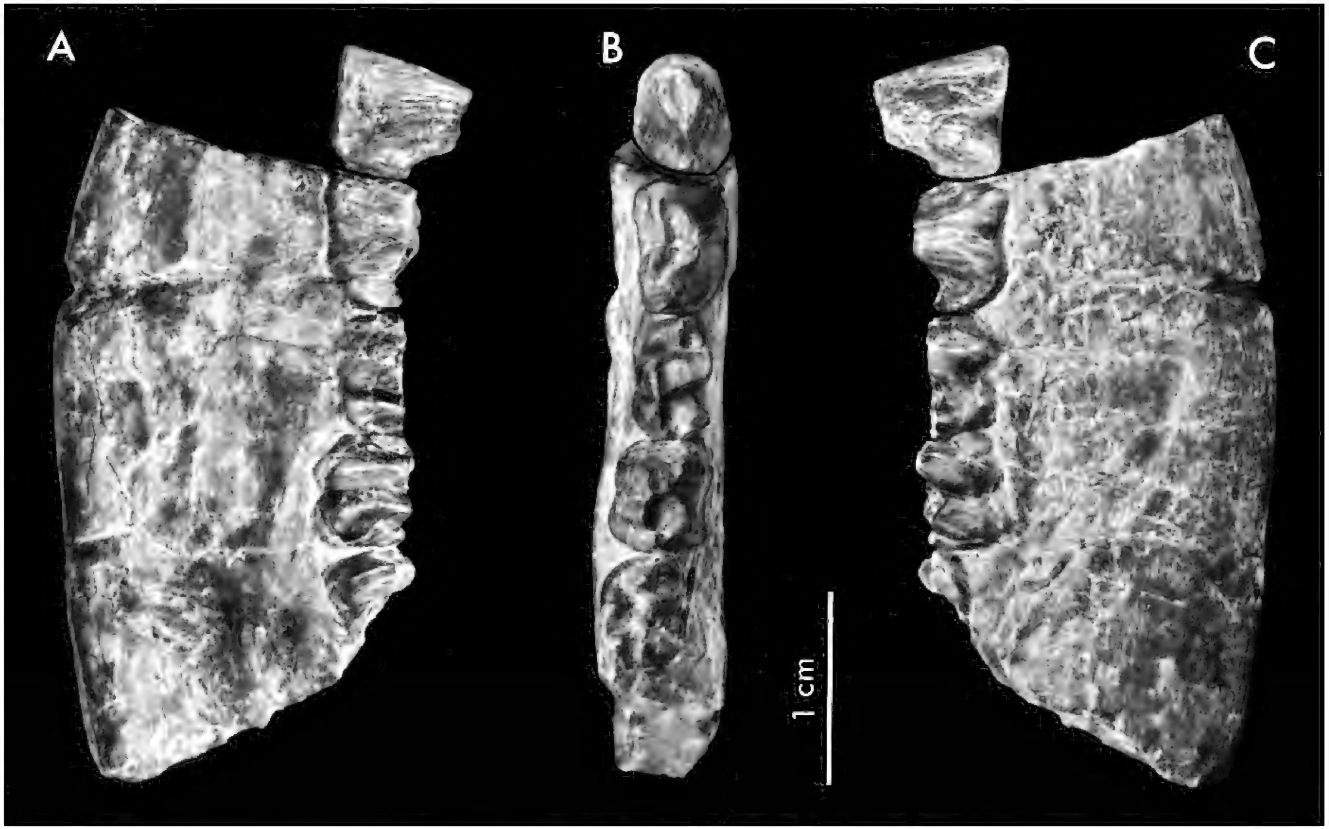

Figure 3 *Goleroconus alfi* gen. et sp. nov. composite photographs of holotype, RAM 7171, right partial dentary with p4–m3 (anterior part), from RAM locality V200120, top of Member 4b of the Goler Formation, approximately 585 m stratigraphically higher in Member 4b than RAM locality V94014, Tiffanian part of Member 4b, Goler Formation, Kern County, California, shown together with RAM 6417, isolated left p3 (photographically reversed for convenience of viewing as a right p3) from RAM locality V94014, Laudate Discovery Site; **A**, lingual views; **B**, occlusal views; **C**, labial views.

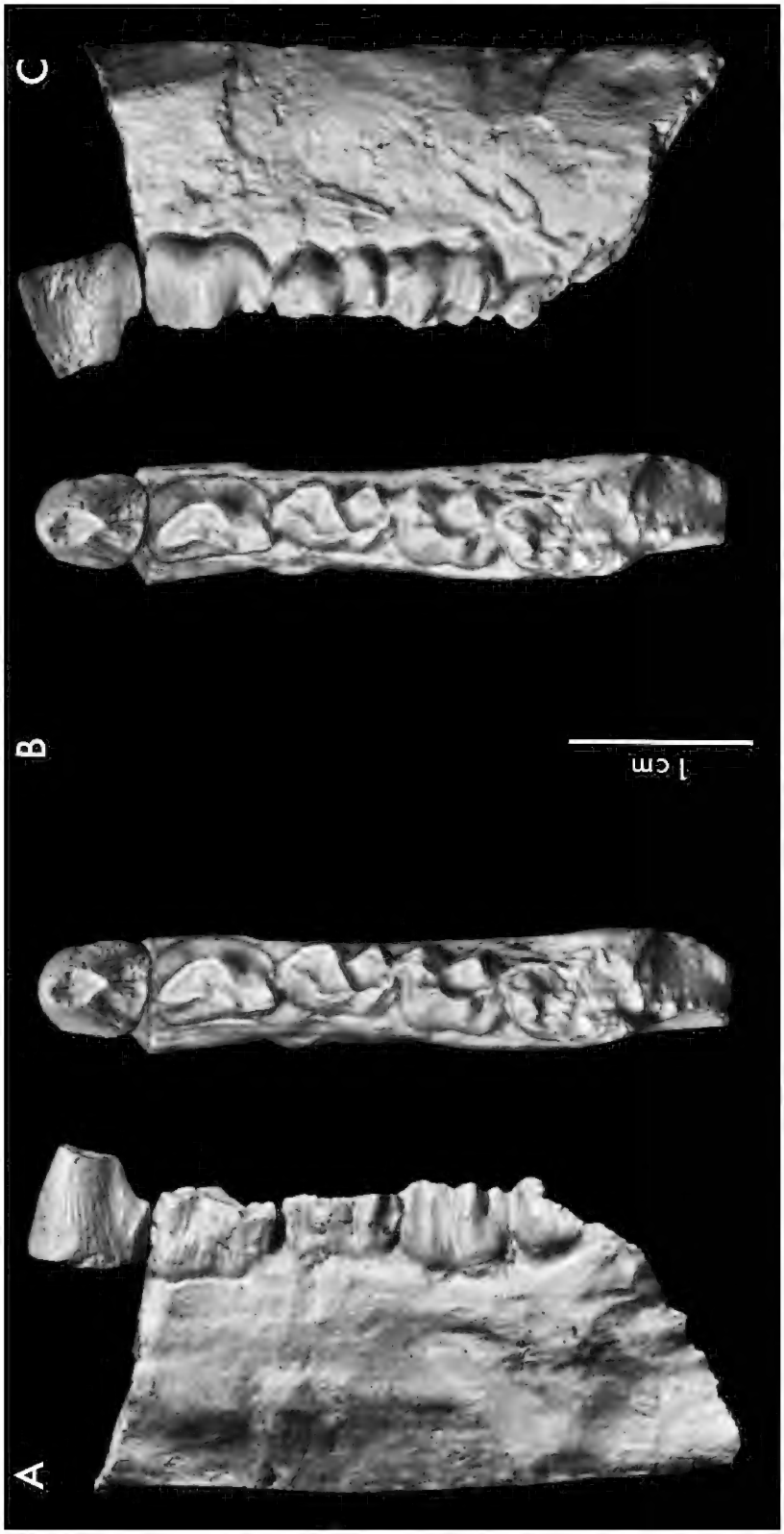

Figure 4 *Goleroconus alfi* gen. et sp. nov. composite photographs of epoxy casts of same specimens as in Figure 3, ventral border of ramus and part of root of p3 deleted; **A**, composite lingual views; **B**, composite stereoscopic occlusal views; **C**, composite labial views.

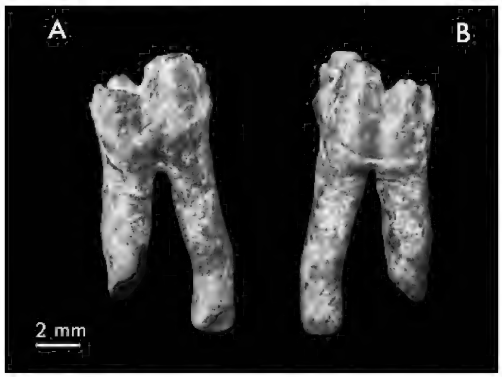

Figure 5 *Goleroconus alfi* gen. et sp. nov. photographs of referred specimen, RAM 6506, right m2, RAM locality V94014, Tiffanian of lower part of Member 4b, Goler Formation, Kern County, California; **A**, labial view; **B**, lingual view.

COMPARISONS. *Goleroconus alfi* differs from *Oxyacodon* Osborn and Earle, 1895, in being larger and by having p4 larger than m1 compared with p4 subequal to or smaller than m1 in *Oxyacodon*. The molar paraconid in *G. alfi* is small and positioned labial to the midline of the tooth, in contrast to *Oxyacodon*, on which the small paraconid is located centrally (except for *Oxyacodon agapetillus* Cope, 1884a, = *Fimbrethil ambaronae* Van Valen, 1978), where paraconid varies in position from central to labial of midline on m2 (see illustrations in Van Valen [1978] and Archibald et al. [1983a]). In *G. alfi*, the m1 trigonid is more elongate relative to the talonid, and the posteriorly facing walls of both the m1 and m2 trigonids are angled strongly posterolingually from protoconid to metaconid compared with the same walls being more directly labiolingually oriented in *Oxyacodon*.

Goleroconus alfi differs from *C. entoconus* (casts of AMNH 3476 and 16424) in that the lower teeth of *G. alfi* are markedly unilaterally hypsodont; p4 is more rectangular and laterally compressed (similar to *Haploconus* Cope, 1882b), with the lingual side of the protoconid weakly concave rather than convex as in *C. entoconus*; p4 has a strong anterolingual crest; the lower molar paraconids are smaller, more labial in position, and more closely appressed to the protoconid than in *C. entoconus*; the lower molar enamel is extended downward noticeably more on the lingual side of the tooth than on the labial side compared with extending roughly equally in *C. entoconus*; the lower molars are without anterolingual cingula. *Goleroconus alfi* is much larger and more hypsodont than *Conacodon cophater* Cope, 1884a, and it lacks lingual cingulids on the molars.

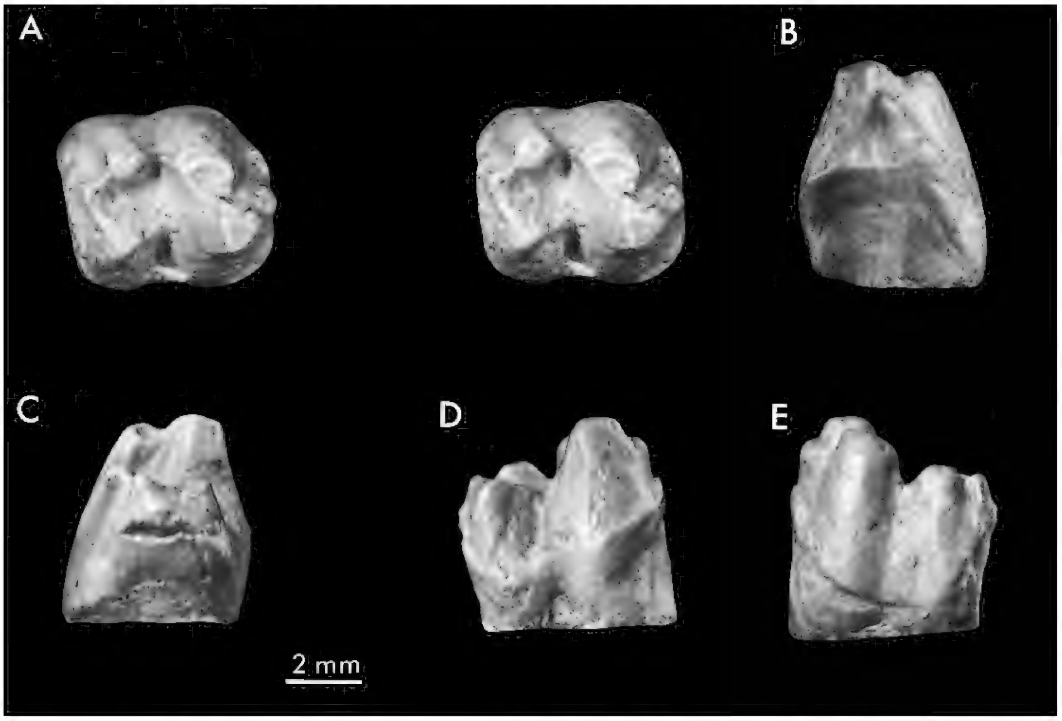

Figure 6 *Goleroconus alfi* gen. et sp. nov. epoxy cast (excluding roots) of same specimen as shown in Figure 5; **A**, stereophotograph, occlusal view; **B**, anterior view; **C**, posterior view; **D**, labial view; **E**, lingual view.

Table 1 *Goleroconus alfi* gen. et sp. nov. measurements (mm) of lower teeth from the Goler Formation, California. Measurements of UCMP 131790 and UCMP 44761 from McKenna (1955, 1960) and McKenna et al. (1987). UCMP 131790 and 44761 were measured with dial calipers; other specimens were measured with an ocular micrometer. **ABBREVIATIONS: L**, length; **W**, width; **WTr**, width of trigonid; **WTa**, width of talonid.

	UCMP 131790	UCMP 44761	RAM 7171	RAM 6506	RAM 6417
p3 L					6.45
p3 W					5.05
p4 L			~6.85		
p4 W			4.7		
m1 L			6.35		
m1 WTr			3.95		
m1 WTa			4.2		
m2 L	5.2		5.75	5.55	
m2 WTr	4.5		4.8	5	
m2 WTa	4.1		5	4.8	
m3 L		~6.0			
m3 WTr		4.4			
m3 WTa		4			

From *Conacodon delphae* Middleton, 1983; *Conacodon harbourae* Middleton, 1983; and *C. kohlbergeri*, *G. alfi* differs in its greater hypsodonty, p4 morphology, and absence of lingual cingulids on the molars. It also differs from *Conacodon utahensis* Robison, 1986, in lacking the anterolingual cingulid on m3.

From *H. angustus* (casts of AMNH 3478 and AMNH 16688), *G. alfi* differs in that its lower teeth are significantly more hypsodont; the p4 has a heel that is smaller relative to the protoconid part of the tooth than in *Haploconus*; the m1 talonid is more broadly basined with cusps less crowded than in *Haploconus*, and its entoconid is slightly less anteriorly displaced relative to the hypoconid; the m1 hypoconulid of *G. alfi* is less posteriorly projecting and slightly closer to the entoconid than to the hypoconid (a similarity to *Conacodon* Matthew, 1897) compared with hypoconulid position axial or closer to hypoconid of *H. angustus* (see Taylor, 1984); a tiny paraconid is present on the lower molars (known from m2–3; some specimens of *H. angustus* are reported to have "slight" paraconids [Gazin, 1941]); the lower molars lack an anterolingual crest that extends from near apex of the metaconid to the anterior cingulum (precingulid).

Compared with *Alticonus gazini* Middleton, 1983, *G. alfi* differs in that the p4 is more laterally compressed than in *Alticonus* Eberle and Lillegraven, 1998, with a slightly concave lingual side; the m2 paraconid is small and labial to midline compared with large and lingual to the midline in *Alticonus*; the m2 and m3 lack the cuspule, present on *Alticonus*, that is anterolingual to the paraconid.

Compared with *Mithrandir gillianus* (Cope, 1882a), (= *Gillisonchus gillianus* Rigby, 1981), *G. alfi* has lower premolars and molars that are strongly hypsodont lingually, p4 without a prominent paraconid, and m1 and m2 without an anterolingual cingulid (seen on *M. gillianus* UNM-B029). *Mithrandir* Van Valen 1978, a proposed subgenus of *Anisonchus* Cope, 1881, was elevated to generic rank by Cifelli (1983), consequently rendering *Gillisonchus* Rigby, 1981, a junior synonym. Archibald (1998) however, retained *Gillisonchus* as a valid genus pending revision of *Anisonchus* Cope, 1881.

In *Tinuviel eurydice* Van Valen, 1978 (photographs and descriptions in Van Valen [1978] and Hunter et al. [1997]), the paraconid on the m2 and m3 is less reduced than in *G. alfi*, and both teeth in *T. eurydice* have a cingular cusp (lacking in *G. alfi*) that is lingual to the paraconid. In *Goleroconus*, the m2 paraconid is buccal to the midline compared with more lingual in *T. eurydice*. The m2 talonid is less anteroposteriorly compressed in *G. alfi*, with the talonid basin less crowded by the surrounding cusps, and the posteriorly facing wall of the m2 trigonid is strongly slanted posterolingually from the protoconid to the metaconid compared with being oriented nearly straight labiolingually in *T. eurydice*.

Differences from *Hemithlaeus kowalevskianus* Cope, 1882d (casts of AMNH 3556 and AMNH 16441), include higher crowned lower teeth in *G. alfi*. The p4 is more anteroposteriorly elongate, is laterally compressed with a concave lingual side, has a larger anterior crest from the protoconid, and has a narrower heel compared with *H. kowalevskianus*. The m1 is relatively more elongate, with a wider and less anteroposteriorly compressed talonid; the m2 enamel extends farther ventrally on the lingual side than the labial side compared with being roughly equal in *Hemithlaeus* Cope, 1882c; and the m2 entoconid is anterior to the hypoconid compared with posterior to the hypoconid in *Hemithlaeus*.

Goleroconus alfi is distinguished from *Anisonchus sectorius* Cope, 1881 (casts of AMNH 3527 and AMNH 16674), by having more hypsodont lower premolars and molars; p4 lacking a large, cuspate paraconid; the lower molars having enamel extended ventrally farther on the lingual side than on the labial side compared with approximately equal extension in *A. sectorius*; the m1 trigonid long relative to the talonid; the m2 and m3 paraconids more reduced in *G. alfi* and the m2 entoconid more anteriorly positioned and close to the metaconid; and the m1 and m2 lacking a posterolingual cingulid.

Anisonchus fortunatus Simpson, 1932, was described from upper teeth only, and it therefore cannot be compared directly with *G. alfi*. However, it is too small to represent the same

taxon. The P4 of *A. fortunatus* is short, indicating that its p4 was also short and thus would be unlike the enlarged p4 of *G. alfi*.

On the basis of m1 and m2, the lower molar paraconid in *G. alfi* contrasts with that of *Ampliconus browni* Middleton, 1983, and *A. antoni* Eberle and Lillegraven, 1998, by being labial to the groove between the protoconid and metaconid. The molar paraconid is reduced and situated on the anterolingual slope of the protoconid compared with being larger and more medial in species of *Ampliconus* Middleton, 1983. The m1 trigonid is more elongate relative to its talonid in *G. alfi*, the m2 paraconid is closely appressed to the protoconid, and the m2 trigonid is approximately the same width as the talonid compared with noticeably wider than the talonid in *Ampliconus* species. In *G. alfi* the m2 entoconid is more anterior than the hypoconid compared with opposite to the hypoconid in *Ampliconus*, and the m2 entoconid is closer to the posterior wall of the trigonid (metaconid) than in species of *Ampliconus*.

Goleroconus alfi is distinguished from *Periptychus* Cope, 1881, by having p4 with less strong ribbing. The lower molars of *Periptychus* are not lingually hypsodont, and they have paraconids that are large and lingual and talonids that are less expanded than in *G. alfi*. The m1 is wider transversely relative to the m2 than in *G. alfi*.

Goleroconus alfi differs from *Ectoconus* Cope, 1884b, in that in the former, the nonmolariform p4 is high crowned and laterally compressed. The lower molars of *G. alfi* are high crowned and lingually hypsodont, and they lack a wide, shelflike buccal cingulid; the lower molar paraconids are labial rather than lingual in position, and the lower molars lack a cuspule lingual to the paraconid.

Goleroconus alfi differs from *Mimatuta* Van Valen, 1978, and *Maiorana* Van Valen, 1978, by its much larger size, with lingually hypsodont p4 and molars. The p4 is longer than m1 in *Goleroconus* compared with subequal or shorter than m1 in *Mimatuta* and *Maiorana*. In *G. alfi*, the molar paraconids are reduced and labial in position, whereas in *Mimatuta* and *Maiorana*, the paraconids are comparatively large and are medial to slightly lingual. The m1 trigonid is more elongate relative to the talonid in *G. alfi*. The talonid notch is closed in *G. alfi* compared with open or only weakly closed in *Mimatuta*. In *G. alfi*, molar lingual cingula are absent, whereas they are commonly present in *Maiorana*.

DESCRIPTION. See Figure 3 (in part) and Figure 4 (in part). The lower fourth premolar is a large tooth, being longer and wearing higher than either the m1 or m2, and it is dominated by a massive protoconid, which extends as a crest anterolinguad, without terminating as a paraconid. The protoconid is vertically striated labially, with the striations being weaker than in *Periptychus*. A crest from the posterolingual side of the protoconid extends posterolinguad to a point just anterior to a small, lingually placed, isolated, heel cusp. The lateral wall of the p4 protoconid is inflated and convex, whereas the lingual wall of the protoconid is concave from the anterior to the posterior crest. The presence or absence of the precingulid is not determinable because of breakage along the lower part of the anterior face of the p4. A lingual cingulum is absent. A posterolabial cingulum runs from the rear of the heel cusp steeply ventrally to terminate at the base of the protoconid.

The m1 is longer but narrower than the m2, wider across the hypoconid and entoconid than across the protoconid and metaconid. The trigonid cusps are heavily worn to a nearly flat surface, with the protoconid and metaconid being therefore merged into a broad posterolingual dentine tract. Another dentine tract extends anteriorly from the protoconid; because of this heavy wear, it cannot be determined whether a tiny paraconid was ever present. The trigonid occupies more than half the length of the tooth. It is worn down nearly to the level of the eroded anterior cingulid (precingulid), which is present on the anterior and anterolabial margins of the tooth but does not extend lingually onto the anterolingual slope of the metaconid. No cingulids or cuspules are present anywhere along the labial or lingual sides of the tooth, including within the hypoflexid. Recalcitrant matrix partially covers the posterior face of the hypoconid, so that the presence of a posterior cingulid is not directly observable. No vertical striations are present on the labial surface of the protoconid. On the talonid, the hypoconid and entoconid are subequal in size and larger than the hypoconulid, which is lingual to the midline and close to the entoconid. The entoconid and hypoconid are directly opposite each other across the midline of the tooth. The entoconid and hypoconulid remain higher in wear than does the hypoconid. The entoconid is close to the posterior wall of the trigonid, and the talonid notch is completely closed by a short crest extending anteriorly from the entoconid to contact the metaconid. The lingual wall of the talonid, formed by the entoconid and its anterior crest, is higher than the labial wall along the crista obliqua. Trending anterolinguad, the cristid obliqua contacts the posterior wall of the trigonid labial to the midline. The talonid basin is shallow. Enamel on the lingual side of the tooth appears to extend farther ventrally than on the labial side.

Aside from breakage of the upper part of the metaconid, the m2 is largely intact on RAM 7171; this breakage occurred after a mold of this specimen was made. The talonid is slightly wider across the base than the trigonid. The cusps show basal inflation on both sides of the tooth, so that the sides slope axially toward the apices of the

cusps. The protoconid and metaconid are of approximately equal breadth but, as seen on the cast of RAM 7171, the protoconid remains higher in wear; the protoconid also remains higher in wear than the metaconid on referred specimen RAM 6506 (see below). The protoconid is offset anterolabially relative to the metaconid; accordingly, the posterior wall of the trigonid angles posterolingually from protoconid to metaconid. A tiny paraconid is present part way up the anterolingual slope of the protoconid, labial to the midline of the tooth. The hypoconid and entoconid are approximately equal to each other in size, and are larger than the hypoconulid, but the entoconid is the tallest talonid cusp. The entoconid is noticeably more anteriorly placed than is the hypoconid and is close to the metaconid, and the talonid notch is closed. The lingual wall of the talonid is distinctly higher than the labial wall along the crista obliqua. A crack marks a slight postmortem posterior displacement of the hypoconulid relative to the hypoconid and entoconid; the hypoconulid is centrally located relative to the anterior–posterior axis of the tooth. A precingulid extends labiad across the base of the paraconid only onto the anterolabial margin of the protoconid, where it ends. The trigonid of the m2 abuts against the talonid of the m1, so that the continuity of the precingulid across the anterior face of the m2 cannot be directly observed. However, in lingual view, a tiny cuspule, or the lingual termination of a cingular shelf, is visible, suggesting labial to lingual continuity of the precingulid. A posterior cingulid descends steeply from high on the labial slope of the hypoconulid across the posterior face of the hypoconid, ending at the posterolabial margin of the hypoconid. As on the m1, a cuspule or a cingular shelf is not present in the hypoflexid.

The m3 of RAM 7171 is almost completely destroyed, preserving only the anterolingual base of the metaconid and the lower part of the paraconid. No anterolingual cingulid is present on the metaconid. A shallow sulcus separates the metaconid from the much smaller paraconid, the latter cusp being similar in size to the paraconid of the m2. The lingual edge of the precingulid is visible at the base of the paraconid.

Specimens referred to *Goleroconus alfi*

Figures 3 (in part), 4 (in part), 5, 6; Table 1

REFERRED SPECIMENS. UCMP 44761 (McKenna, 1955:514), left dentary fragment with m3; UCMP 131790 (McKenna et al., 1987: fig. 5), left m2; UCMP 49487 (McKenna, 1960: figs. 3c and 3d), fragmentary right m3; and RAM 6506, right m2, and RAM 6417, left p3, reported here for the first time.

LOCALITY OF REFERRED SPECIMENS. All referred specimens are from RAM locality V94014 (= UCMP locality V5252), which is located stratigraphically near the base of Member 4b of the Goler Formation (Fig. 2).

DESCRIPTION OF REFERRED SPECIMENS. The m2s (RAM 6506 and UCMP 131790) are the only teeth from RAM locality V94014 that can be usefully compared with the same tooth on the holotype of *G. alfi*, RAM 7171; no p4s or m1s have been recovered from RAM locality V94014, and the two m3s from that locality can be compared only with the broken, fragmentary m3 trigonid on RAM 7171. The m2s from RAM locality V94014 are very similar to the m2 of the holotype dentary, differing slightly in size and in minor morphological details. The significance of these differences, whether at the individual or species level, cannot presently be determined. However, the apparently considerable stratigraphic separation of RAM localities V200120 and V94014, on the order of 585 m (see Fig. 2), coupled with the evidence of significant time difference between RAM localities V98012 (Ti2-3) and V200202 (Ti4?) in Member 4b of the Goler Formation (Lofgren et al., 2008), certainly raises the possibility that these morphological differences could have species significance. For this reason, we choose to describe RAM 6506, UCMP 131790, and the other teeth from V94014 separately from RAM 7171, being fully cognizant of the possibility that when more complete material is recovered from V94014, the differences between these specimens might be found to be nothing more than individual variation. We have included with the original dentary (McKenna, 1955) and the m2s in *G. alfi*, three additional teeth from RAM locality V94014: RAM 6417, a probable p3, and UCMP numbers 44761 and 49487, left and right m3s. Our rationale for placing these additional teeth in *G. alfi* includes evidence for increased hypsodonty and size compatibility with the teeth of the holotype.

We believe that isolated tooth RAM 6417 is a left p3 (Figs. 3 and 4, in part). It is a large tooth, consisting mainly of a massive protoconid worn into an oval of dentine by orthal occlusion at the apex. Weak vertical striations occur on both the labial and lingual sides; the labial ones are partially obscured by some erosion of the enamel. The labial side of the protoconid is convex from apex to base, whereas the lingual side is straighter, except at the base, where it is slightly inflated. A narrow ridge descends steeply down the posterior side of the protoconid to end at the central, high point of a narrow, compressed heel. There is no anterior crest. A narrow cingulid descends very steeply anterolingually along the posterior margin of the tooth, ending before reaching the base of the tooth. The posterobuccal margin of the p3 is pitted, but a weak, steep posterobuccal cingulid that did not reach the base

of the tooth appears to have been present. No cingulids are present along the buccal or lingual margins of the protoconid.

We also believe RAM 6417 is the p3 of *G. alfi*. Compared with p3s of similar periptychids, RAM 6417 is higher crowned than *Ectoconus*, laterally inflated, and without a basined heel compared with *H. angustus*; lacks a paraconid compared with *A. gazini*, *M. gillianus*, and *A. sectorius*; and is less inflated with less strong ribbing compared with *Periptychus*.

RAM 6506 (see Figs. 5 and 6) and UCMP 131790 are both similar to the m2 of RAM 7171 in that they are unilaterally hypsodont, with the enamel on the lingual side of the tooth extending more ventrally than enamel on the labial side. They have basally inflated cusps and a small paraconid on the anterolingual slope of the protoconid (labial to the midline of the tooth), and the entoconid is the tallest talonid cusp. The talonid notch is closed. A lingual cingulid is absent. RAM 6506 and UCMP 131790 differ from RAM 7171 by having the trigonid slightly wider than the talonid, rather than vice versa, and by the enamel on the anterior margin of the metaconid being less extended ventrally than in RAM 7171. Unlike in RAM 7171, a short, anterolingual part of the precingulid is present, and a short cingulid can be present in the hypoflexid (RAM 6506 only). Buccal cusps, particularly the hypoconid, show slightly less buccal curvature on RAM 6506 and UCMP 131790. The entoconid is less anteriorly displaced toward the metaconid, with the result that the notch between the metaconid and entoconid is deeper than on RAM 7171. In RAM 6506 and UCMP 131790, the cristid obliqua shows a more medial trend toward the posterior wall of the trigonid than in RAM 7171, and the hypoconulid is slightly lingual of the midline of the tooth, nearer the entoconid than the hypoconid.

RAM 6506 is nearly identical to UCMP 131790 in most details, described previously by McKenna et al. (1987), but it shows slightly greater wear, suggesting that it belongs to a different individual. Individual variation is revealed in the position of the paraconid. In both specimens the paraconid is labial to the notch between the protoconid and metaconid, residing on the anterior slope of the protoconid. However, on RAM 6506 the paraconid is more strongly labial, almost directly anterior to the protoconid apex, whereas on UCMP 131790, the paraconid is immediately adjacent to the notch. The sharp crest high on the anterior face of the metaconid on UCMP 131790 is not seen on RAM 6506, probably because of the greater wear on the latter specimen. A cingular cuspule is present on the posterobuccal margin of the protoconid of RAM 6506, and it extends rearward into the hypoflexid as a faint shelf before terminating against the anterior slope of the hypoconid. This hypoflexid cingulid is not present on UCMP 131790, but in labial view (see McKenna et al., 1987:fig. 5), the enamel is seen to be eroded in this area.

Details of the m3 have been described previously (McKenna, 1955, 1960), and no new specimens have been collected since then.

DISCUSSION

Among the periptychids, *G. alfi* is most similar to *Haploconus* and *Conacodon*. Similarities to *Haploconus* include a large, laterally compressed, somewhat rectangular p4, on which the protoconid extends anterolingually as a short crest. The m1 of *G. alfi* is also elongate and slightly laterally compressed. In this respect, it resembles the narrow m1 of *Haploconus*. *Goleroconus alfi* has a tiny, labial molar paraconid that is appressed to the anterolingual slope of the protoconid and is connected to the protoconid apex by a short ridge (paracristid). Whereas *Haploconus* generally lacks a molar paraconid altogether (see diagnosis), it does have a paracristid (longest on m1 [Taylor, 1984]) that descends slightly anterolingually from the protoconid apex and that bears a striking resemblance to the molar paracristid on *G. alfi*. On m1 and m2 of the type specimen of *G. alfi*, the entoconid is very close to the posterior surface of the metaconid (the entoconid is less closely appressed to the metaconid on the referred specimens of *G. alfi*), resulting in complete closure of the talonid notch. In *H. angustus* (casts of AMNH 3478 and 16688), the entoconid is also anteriorly displaced close to the metaconid, and the talonid notch is closed by crests from each cusp. The m3 of *G. alfi* has a subsidiary talonid basin, as does *Haploconus* (McKenna, 1960). *Goleroconus alfi* is similar to *Conacodon* in having a laterally inflated p3 without a basined heel (referred specimen—the holotype of *G. alfi* lacks the p3). Small molar paraconids are present in both *Conacodon* and *G. alfi* (uncertain for m1 of *G. alfi*) but are medial in *Conacodon* and labial in *G. alfi*. The talonid cusps on m1 (and to a lesser degree m2) of *Conacodon* and *G. alfi* are less crowded than in *Haploconus*, with the hypoconulid being less posteriorly projecting and slightly closer to the entoconid than to the hypoconid. Unlike those of *Haploconus*, the molars of *Conacodon* and *G. alfi* are without a precingulid that extends onto the anterolingual slope of the metaconid to ascend to near the apex of that cusp.

In two recent classifications of the Periptychidae (McKenna and Bell, 1997; Archibald, 1998), the family is subdivided into three subfamilies—Periptychinae, Anisonchinae, and Conacodontinae—plus several genera *incertae sedis*. In considering the subfamilial placement of *G. alfi*, we note that *Conacodon* is in the Conacodontinae and *Haploconus* is in the Anisonchinae—as those

subfamilies are defined. The Conacodontinae comprises *Conacodon* and *Oxyacodon*. *Oxyacodon* and *Conacodon* share derived similarities in the upper teeth; Conacodontinae is in fact, diagnosed on the basis of upper dental features (large, lingually expanded M1–3 hypocone; P3 protocone absent; tendency for precingulum to contact hypocone across the protocone [Archibald et al., 1983b; Archibald, 1998]). The Anisonchinae comprises *Anisonchus*, *Haploconus*, *Mithrandir* (= *Gillisonchus*), and other genera, depending on the author. Anisonchinae is defined on the basis of a few characters of both the upper and lower teeth (small size; posterior premolar paraconids large or absent (because of fusion with the trigonid); and P3 protocone present or absent—see Archibald (1998). The upper molars of *Haploconus* are not so specialized as those of the two conacodontine genera.

The current diagnoses for Conacodontinae and Anisonchinae are not mutually exclusive and are inadequate to determine to which subfamily *Goleroconus* belongs. Because of the similarities seen in the lower teeth of *Goleroconus* to both *Conacodon* and *Haploconus* and because upper teeth are presently unknown for *Goleroconus*, we cannot be sure if *Goleroconus* belongs in the Conacodontinae or if it is more closely related to *Haploconus* of the Anisonchinae. Eberle and Lillegraven (1998) abandoned use of Conacodontinae and returned to a two-subfamily Periptychidae on the grounds that separation of *Oxyacodon* and *Conacodon* into their own groups resulted in making the Anisonchinae paraphyletic. That is, the resulting Anisonchinae would include primitive genera, such as *Mimatuta*, that were no more closely related to other anisonchines than they were to *Oxyacodon* and *Conacodon*, and it would also include the genus *Ampliconus*; Eberle and Lillegraven (1998) considered *Ampliconus* morphologically intermediate between primitive anisonchines and conacodontines. In his analysis of the Periptychidae, Archibald (1998) removed *Mimatuta* from the Anisonchinae and placed it as the sister taxon to other periptychids, but he did not discuss *Ampliconus* because it had previously been referred to only in dissertations. The similarities that *G. alfi* shares with *Conacodon* and *Haploconus* suggest that the two latter genera might be more closely related than indicated by the current three-subfamily structure, a suggestion previously made by Rigby (1981). Archibald et al. (1983b) noted several similarities of *Haploconus* to the Conacodontinae but regarded them as parallelisms. When found, upper teeth of *Goleroconus* will surely shed light on this issue.

CONCLUSIONS

1. *Goleroconus alfi* gen. et sp. nov. is an advanced, small periptychid. Similar to Puercan *C. entoconus* and to Torrejonian species of *Haploconus*, *G. alfi* has added unilateral hypsodonty to its apomorphies, and it possesses a lingually concave wall of the p4 trigonid.
2. The occurrence of *G. alfi* in rocks of Tiffanian age in the upper part of the Goler Formation of California is a significant geographic range extension for small periptychids. The species is unknown from Paleocene strata of the Rocky Mountain states, Texas, Mexico, or Canada.
3. Small periptychids are better known from southern than northern localities in the United States. *Goleroconus alfi* fits that pattern.

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IN MEMORIAM

Dr. Malcolm C. McKenna 1930–2008

Dr. Malcolm C. McKenna passed away on March 3, 2008. Malcolm authored two of the chapters in this volume and assisted in reviewing others. He taught at the University of California, Berkeley, and at Columbia University, was Frick Curator of Vertebrate Paleontology at the American Museum of Natural History, and recipient of both the Paleontological Society Medal and the Romer-Simpson Medal of the Society of Vertebrate Paleontology. Malcolm McKenna will be remembered for his extensive work on virtually all mammalian groups and for being a great interdisciplinary thinker, always keeping on top of the latest developments in stratigraphy, geology, and plate tectonics, and incorporating these fields into mammalian paleontology.

Magnetic stratigraphy of the Eocene to Miocene Sespe and Vaqueros formations, Los Angeles and Orange counties, California

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ABSTRACT. The middle Eocene to lower Miocene age Sespe and Vaqueros formations in northern Orange County and northwestern Los Angeles County, California, USA, yield many important vertebrate and invertebrate fossils. These include Uintan (late middle Eocene) and Arikareean to Hemingfordian (late Oligocene to early Miocene) land mammals in the Sespe Formation, and important marine mammals (including the oldest sirenians and desmostylians in California and many early whales) and mollusks of the *Turritella inezana* Zone in the Vaqueros Formation. Paleomagnetic analyses of five important fossil-bearing sections in northern Orange County and one in Los Angeles County were undertaken to determine the age of these fossils and to supplement previous paleomagnetic studies of the Sespe and Vaqueros sequence. More than 225 samples were collected and subjected to both thermal and alternating field demagnetization. Although most samples had a slight chemical remanence overprint resulting from goethite, their characteristic remanence was held mostly in magnetite with little hematite (despite the red color of many rocks). Both normal and reversed polarities were documented and passed reversal tests, demonstrating that the overprints had been removed and a primary or characteristic remanence revealed. There was no evidence of statistically significant tectonic rotation or translation in the Orange County rocks, but the Los Angeles County rocks showed a clockwise tectonic rotation of about 47 ± 13° (typical of other results from the western Transverse Ranges). Two sections (Jamboree Road and Santiago Canyon Road) yield late Uintan mammals in rocks of reversed polarity, which correlate with Chron C18r (40.0–41.1 Ma) on the basis of comparisons with Sespe faunas and magnetic stratigraphy of Simi Valley, Ventura County, California. The upper part of the Santiago Canyon Road and the Irvine Lake Sespe Formation sections probably correlates with Chrons C10n–C10r (28.3–29.5 Ma) on the basis of their early Arikareean mammals. The lower Piuma Road section in the Santa Monica Mountains correlates with Chrons C8n–C9r (26–28.2 Ma) on the basis of early Arikareean mammals and a date of 27.2 ± 0.2 Ma for a tuff just above the fossil-bearing interval. The upper Piuma Road section probably is assignable to Chrons C5Er–C6Ar (18.6–21.9 Ma) on the basis of early Hemingfordian land mammals at the top and a date of 21.1 ± 0.2 Ma near the base. The Laguna Canyon Vaqueros Formation sections, which yield whales, desmostylians, and sirenians, were mostly normal in polarity (with a short reversed zone at the base), but their correlation is less certain. They probably correlate with Chrons C5Dn–C5Er (17.5–19.0 Ma; early Miocene) on the basis of the occurrence of early Hemingfordian mammals in the underlying Sespe redbeds.

INTRODUCTION

The Sespe and Vaqueros formations are distinctive and widespread middle Tertiary rock units found throughout central and southern California. First defined by Watts (1897) and based on exposures in lower Sespe Creek near Fillmore, Ventura County, California, the distinctive red sandstones and mudstones of the Sespe Formation crop out in many places from northern Santa

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Barbara County to southern Orange County, as well as on Santa Rosa Island in the Santa Barbara Channel. This formation also occurs in the subsurface. In some places, the Sespe Formation exceeds 1,700 m in thickness, although most exposures are discontinuous and highly faulted.

In most places, the Sespe Formation is conformably overlain by the widespread gray marine sandstone that is known as the Vaqueros Formation. Originally based on exposures in the Santa Lucia Range near King City (Hamlin, 1904), the Vaqueros Formation crops out widely from the type area all the way to southern Orange County (Loel and Corey, 1932). The Vaqueros Formation has long been known for its abundant shallow-water marine molluscan fauna that includes such taxa as *Turritella inezana* Conrad, 1857, and *Rapana vaquerosensis* Arnold, 1907, which were the basis for the Vaquerosian molluscan stage (Loel and Corey, 1932; Addicott, 1972). Although the color differences between these two formations are easily mapped in most places, in some places, the contact is gradational, and in others redbeds interfinger with gray shallow marine sandstones.

Most studies of the Sespe and Vaqueros sequence have focused on the outcrops and fossils from the Transverse Ranges and farther north (Fig. 1A). For example, outcrops of the Sespe and Vaqueros sequence are widespread in the Santa Monica Mountains (Yerkes and Campbell, 1979, 1980; Howard, 1988; Dibblee, 1993). The Piuma Road section (Fig. 1B) in this study is one of the thickest and best dated Sespe and Vaqueros sequences in the Santa Monica Mountains. In addition, the Santa Ana Mountains and Laguna Hills in Orange County (Fig. 1C) also produce a thick sequence of land mammal–bearing Sespe Formation redbeds that are overlain by marine mollusk–bearing Vaqueros Formation strata. These beds were mapped and described by a number of geologists (Vedder et al., 1957; Schoellhamer et al., 1981; Belyea, 1984; Howard, 1988; Belyea and Minch, 1989). Here, the Sespe and Vaqueros sequence ranges in thickness from 300 to 900 m, and it looks very similar to the Sespe and Vaqueros outcrops that are 160 km away in Ventura County. Because the contact is in most places gradational, Schoellhamer et al. (1981) mapped them as "Sespe and Vaqueros undifferentiated," as have all later workers (e.g., Lander, 1994a, 1994b; Lucas et al., 1997).

Stock (1920, 1930, 1948) and Kew (1934) were the first to report fossil land mammals from the Sespe Formation, and these faunas soon became critical to our understanding of mammalian evolution on the Pacific Coast of North America. In Ventura and Santa Barbara counties, late Uintan and Duchesnean (late middle Eocene) and early Arikareean (late Oligocene) mammals have been found. The Sespe Formation is the only depositional sequence in North America where land mammal faunas assignable to these land mammal ages occur in stratigraphic succession, but faunas from the intervening Chadronian (late Eocene) and Orellan–Whitneyan (early Oligocene) land mammal ages are missing. Originally, it was thought that the Sespe Formation spanned the entire late Uintan through early Arikareean interval. Subsequent analysis has shown that upper Eocene and lower Oligocene rocks are missing from the Sespe Formation wherever it occurs (Prothero et al., 1996), with an unconformity spanning at least 7 million years occurring between the middle Eocene and late Oligocene portions of the section. The middle Eocene megasequence of the Sespe Formation was deposited in an alluvial coastal plain setting during a period of major marine regression (Howard, 1988), a regression that culminated in the largest eustatic drop of sea level in the entire Phanerozoic time interval. The lowered base level led to a period of erosion that removed a great deal of the Sespe Formation. The second megasequence of the Sespe Formation represents backfilling of the basin that coincided with a major transgression (Howard, 1988). Lander (1994a, 1994b, 1997, 2002b) and Lander et al. (2001b), however, consider the regression and transgression to reflect collisional and extensional tectonic events along the continental margin.

In Orange County, paleontological studies of Sespe Formation vertebrate assemblages began in 1947. However, these assemblages from Orange County were less extensive than those that had been documented in the Sespe Formation to the north until recent excavations for new housing and freeway projects produced many large collections of fossils (Whistler and Lander, 2003). These collections reveal that the Sespe Formation of Orange County yields fossils of late Uintan, Duchesnean (middle Eocene), Arikareean (late Oligocene), and even early Hemingfordian (early Miocene) age (summarized in Prothero and Donohoo, 2001; Whistler and Lander, 2003). Thus, outcrops of the Sespe Formation in Orange County span a greater age range than any other exposures of the unit (from about 41.0 Ma to as young as 17.5 Ma).

The Vaqueros Formation exposures in Orange County received little attention prior to the study by Schoellhamer et al. (1981). Recent excavations related to construction, however, have produced abundant Vaquerosian age molluscan faunas, as well as an important assemblage of marine mammals, many of which are still in preparation and some not yet reported. Noteworthy are 11 associated sirenian skeletons (the oldest in California; Barnes, 2003e), a primitive desmostyline desmostylid (the oldest in California; Barnes, 2003e), and several species of whales (Barnes, 2003b, 2003e), including a very primitive squa-

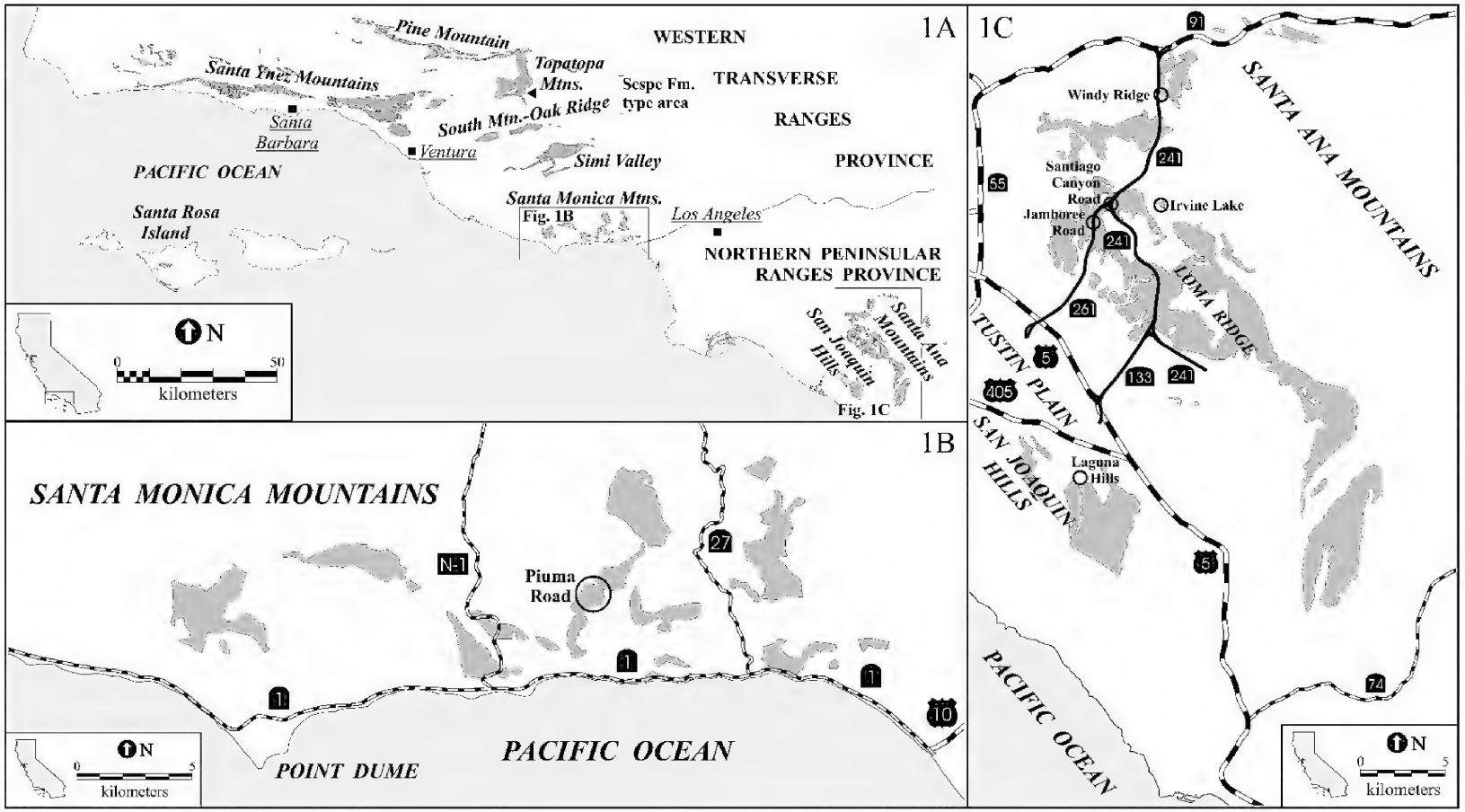

Figure 1 A, Index map showing major geographic features and outcrops of the Sespe and Vaqueros formations (shaded areas) in southern California; B, enlargement showing location of paleomagnetic section in western Los Angeles County; C, enlargement showing location of paleomagnetic sections in northern Orange County.

lodontid odontocete (Kearin and Barnes, 2001; Dooley et al., 2004a, 2004b), an archaic tooth-bearing mysticete (Angulo et al., 2004), several very primitive baleen-bearing mysticetes (Barnes, 2003c, 2003d; Deering et al., 2004), and a platanistid dolphin that is referable to either *Allodelphis pratti* (Wilson, 1935) or a new species of *Allodelphis* (Barnes, 2003a, 2007; Barnes et al., 2003; Deering et al., 2003). However, the primary age constraint on these faunas is the Vaquerosian age mollusks, which appear to range through the entire late Oligocene and early Miocene, or 17 to 28 Ma, and therefore are not sufficiently age-diagnostic for high-resolution dating (Prothero and Hoffman, 2001; Prothero and Donohoo, 2001).

The magnetostratigraphic correlations reported by Prothero and Donohoo (2001) and Prothero et al. (1996) were successful in dating important fossil-bearing outcrops in the Santa Ana Mountains and in Ventura County. A new paleomagnetic sampling program was undertaken subsequently in hopes that additional Sespe and Vaqueros formation outcrops also could be dated by the same method. Preliminary results of this research were presented by Ludtke et al. (2003a, 2003b) and integrated with lithostratigraphic and biostratigraphic data presented by Calvano et al. (2003a, 2003b).

METHODS AND MATERIALS

The stratigraphic sections in Orange County were measured and described by Calvano during salvage paleontology that was conducted in support of major construction projects. The Piuma Road section was measured by E. Bruce Lander and John M. Alderson. A map of the localities is shown in Figure 1. Paleomagnetic samples were collected in the fall of 2002 and the spring of 2003 with the use of hand tools to recover oriented blocks of rock. Three separate blocks were collected at each site. Oriented cores were drilled from the blocks with a drill press, or were prepared from smaller pieces of rock with Zircar aluminum oxide ceramic. The samples were measured on a 2G cryogenic magnetometer at the California Institute of Technology with an automatic sample changer. After measurement of natural remanent magnetization (NRM), each sample was demagnetized in alternating fields (AFs) of 25, 50, and 100 gauss then thermally demagnetized in 100°C steps from 300°C to 600°C to remove any chemical remanence held by iron hydroxides such as goethite and to determine whether any remanence held by hematite remained after the Curie point of magnetite (580°C) had been exceeded.

About 0.1 g of powdered rock from each of several samples was subjected to increasing isothermal remanent magnetization (IRM) to determine their IRM acquisition behavior, which is useful in determining whether the remanence is held in magnetite or hematite. The samples also were AF demagnetized twice: once after having acquired an IRM produced in a 100-mT (millitesla) peak field and once after having acquired an anhysteretic remanent magnetization (ARM) in a 100-mT oscillating field. Such data are useful in conducting a modified Lowrie–Fuller test (Pluhar et al., 1991), which helps to determine whether single-domain or multidomain magnetic grains are present.

Extensive fossil collections were made by Calvano. Approximately 50-kg samples were collected from numerous exposed red beds in each of the Orange County Sespe and Vaqueros formation sections. No fossils were visible on the surface, so samples were collected from convenient spots in each bed. A total of 3,200 kg was collected and processed for microfossils. Productive beds at critical levels in the section were resampled. Initial processing of samples through 30-mesh box screens, followed by heavy liquid separation and picking of concentrate, was performed by Calvano. The small fossil mammals in Orange County were identified by David P. Whistler, Hugh M. Wagner, or Steven L. Walsh (see Whistler and Lander [2003] for faunal summaries). Much of this work was an extension of earlier investigations that were conducted as part of the paleontologic salvage program for the Eastern Transportation Corridor (Lander, 2002c). The Los Angeles County samples were collected by Lander and John M. Alderson and processed by David P. Whistler, who also identified the small mammals.

ABBREVIATIONS

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RESULTS

ROCK MAGNETIZATION

Orthogonal demagnetization ("Zijderveld") plots of representative samples are shown in Figure 2. Limited response to AF demagnetization suggests that some remanence is held in a high-coercivity mineral such as hematite or in an iron hydroxide such as goethite. The abrupt decrease in intensity at 300°C (above the dehydration temperature of goethite) suggests that much of this high-coercivity remanence is indeed held in iron hydroxides. In a few samples (e.g., Fig. 2A), thermal demagnetization at 300°C removed a slight overprint to reveal a stable normal direction. In nearly every sample, the remanence was completely gone by 500°C, a result that is consistent with a mineral such as magnetite, which has a Curie temperature

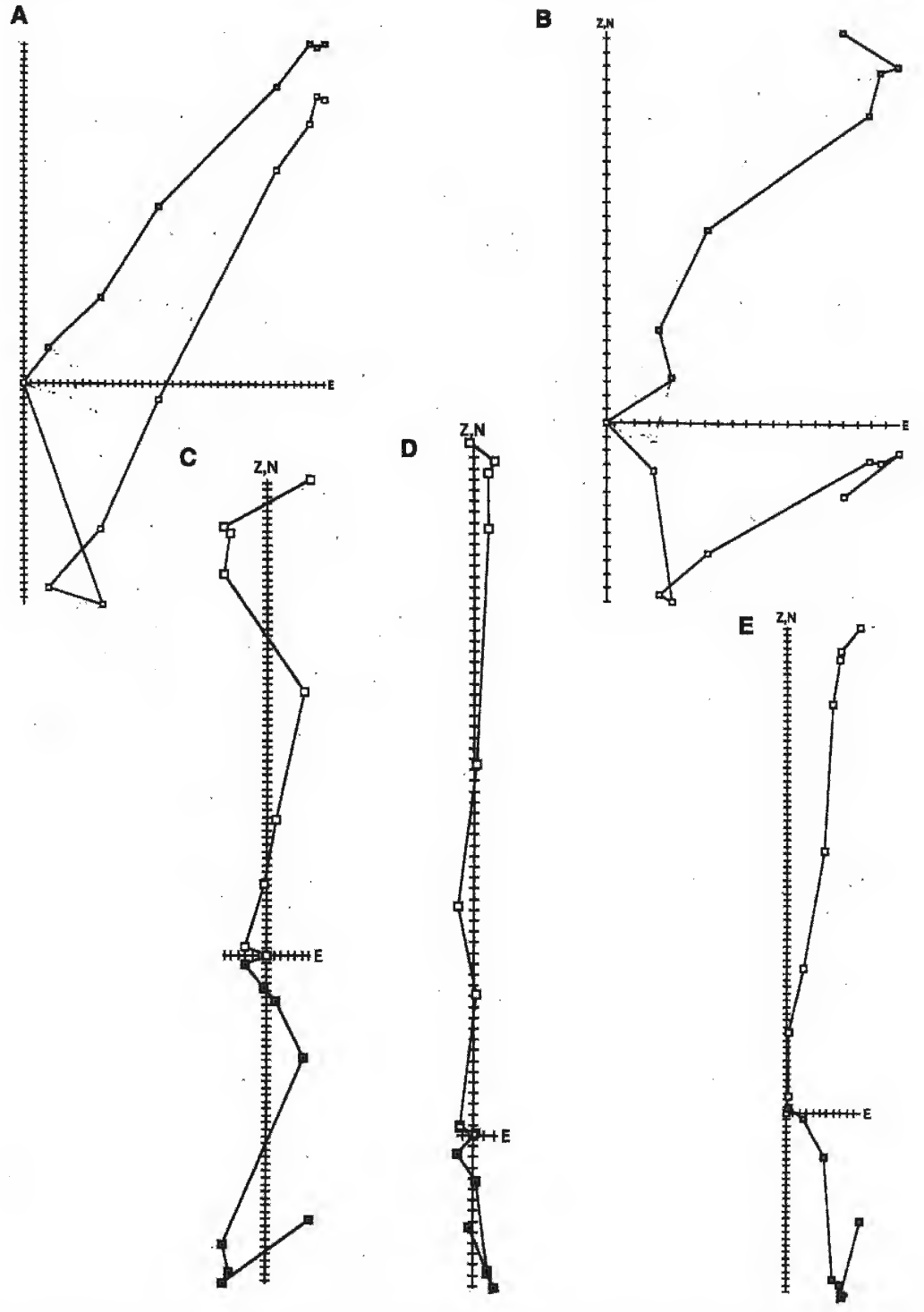

Figure 2 Orthogonal demagnetization plots of representative samples from the Sespe and Vaqueros formations (tilt-corrected). Solid squares indicate horizontal component; open squares indicate vertical component. First four steps are alternating field steps of natural remanent magnetization (NRM) 25, 50, and 100 gauss, followed by thermal steps of 300, 400, 500, and 600°C. Each division = 10^{-6} emu. Samples **A** and **B** show a clockwise tectonic rotation seen in the Piuma Road samples; samples **C**, **D**, and **E** do not show the type of rotation that is typical of rocks in Orange County, California.

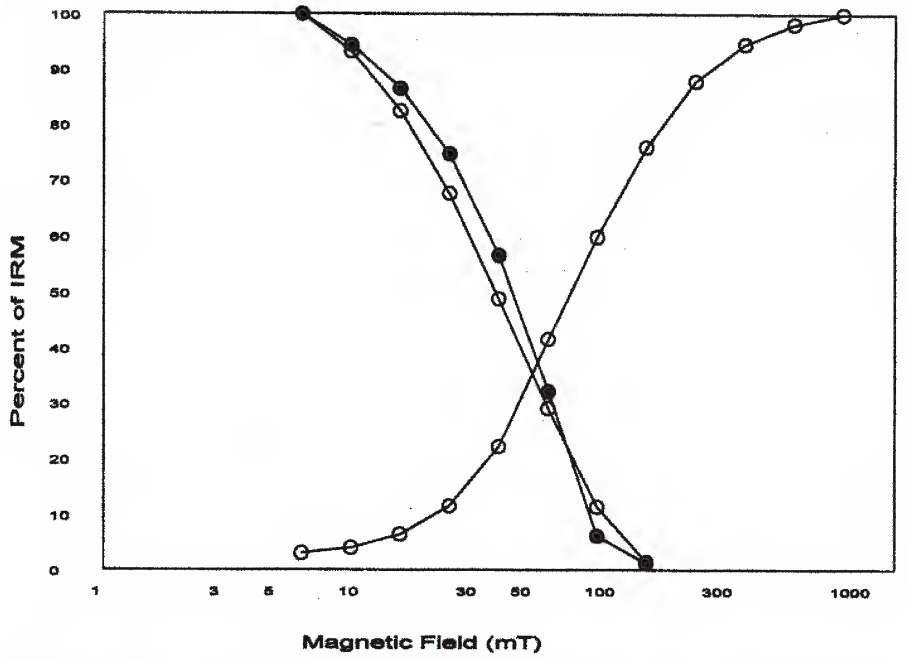

Figure 3 IRM acquisition (ascending curve on right) and Lowrie–Fuller test (two descending curves on left) of representative powdered samples from the Sespe and Vaqueros formations in Orange County, California. Open circles = IRM; solid circles = ARM.

of 580°C. Thus, it seems likely that the remanence is held mainly in magnetite, with only minor chemical overprinting by goethite or other iron hydroxides, and not in hematite, despite the red color of many of the rocks. The red color results largely from goethite, in which remanence was removed by dehydration to hematite in the first thermal demagnetization step.

A representative IRM acquisition analysis is shown in Figure 3. Most samples showed near saturation at 300 mT, suggesting that the remanence is held largely in magnetite, although the continuing increase in IRM suggests some hematite was also present. In most samples, the ARM was more resistant to AF demagnetization than the IRM, suggesting that the remanence is held in single-domain or pseudo–single-domain grains (Pluhar et al., 1991).

Most of the samples showed a direction that pointed north and down or south and up at NRM and showed only a single component of magnetization that decayed steadily to the origin (Fig. 2B–E). Because these data are corrected for dip, the south and up direction clearly is a reversed direction that has undergone clockwise rotation. A few samples (Fig. 2A) had a slight overprint but showed the characteristic normal direction by 300°C. Thus, it is apparent that the direction is a primary or characteristic remanence and not an overprint or later magnetic component.

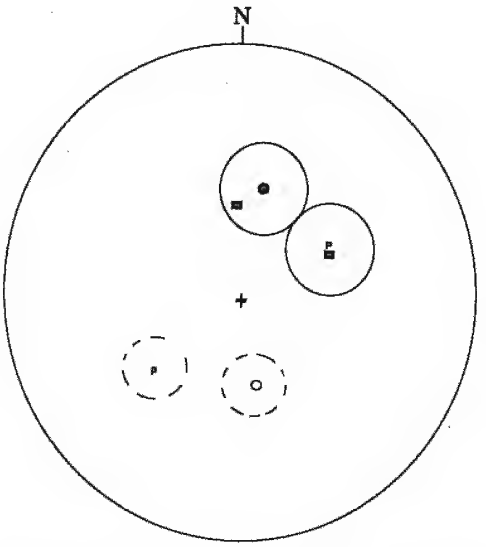

Figure 4 Stereoplot of mean poles and circles of confidence for the data discussed in this study. Solid circles indicate lower hemisphere projections of Orange County, California, samples; dashed lines and open circles indicate upper hemisphere projections. Solid squares indicate mean of reversed samples projected through the origin to the lower hemisphere. "P" and "p" indicate means of rotated Piuma Road normal and reversed samples, respectively.

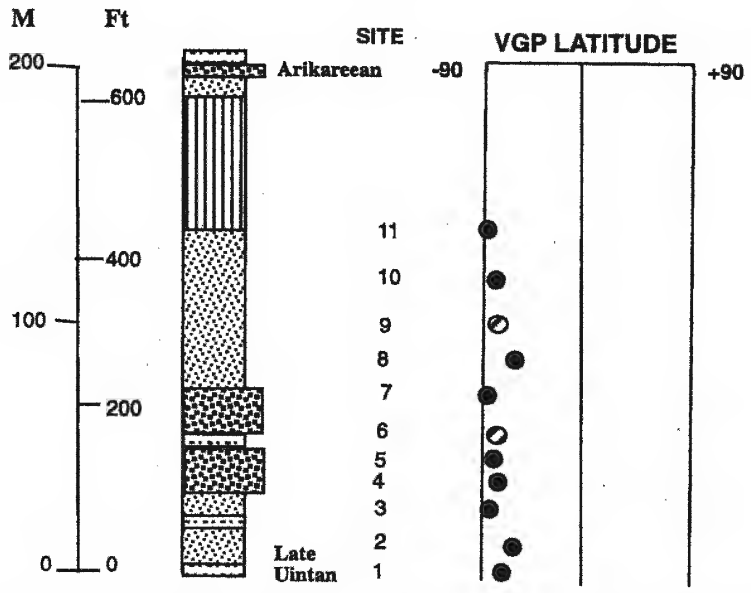

Figure 5 Lithostratigraphy and magnetic stratigraphy of lower part of the Sespe Formation along the south side of Highway 261 and south of Jamboree Road, San Joaquin Hills, Orange County, California. The upper part of the section was previously published by Prothero and Donohoo (2001:fig. 5). Solid circles indicate Class I sites (Opdyke et al. 1977), which are statistically distinct from a random distribution at the 95% confidence level; circles with diagonal slash pattern are Class II sites, in which one sample was missing, so site statistics could not be calculated. VGP latitude = virtual geomagnetic pole latitude of each site.

That the direction is a primary or characteristic remanence is confirmed by the reversal test (Fig. 4). The mean for the 45 normal samples in Orange County is $D = 18.4$, $I = 47.7$, $k = 7.3$, $\alpha_{95} = 8.5$; the mean for the 94 reversed samples in Orange County is $D = 171.3$, $I = -52.4$, $k = 9.2$, $\alpha_{95} = 5.1$. These directions produce overlapping circles of confidence and therefore are antipodal within confidence limits (Fig. 4). Inverting the reversed directions through the origin, the mean for both formations is $D = 0.5$, $I = 51.6$, $k = 7.9$, $\alpha_{95} = 4.6$ ($n = 139$). The mean inclination of 51.6° produces a paleolatitude of 32°, which is indistinguishable from the present latitude, so there is no evidence of northward translation of these rocks. The mean declination of 0.5° also is statistically indistinguishable from the present declination, so there is no evidence of tectonic rotation (as already observed by Prothero and Donohoo [2001] elsewhere in Orange County).

The data from Piuma Road section, however, do show a tectonic rotation, as would be expected from rocks in the western parts of the Transverse Ranges. The mean for the eight normal samples is $D = 64.2$, $I = 42.7$, $k = 17.2$, $\alpha_{95} = 13.8$; the mean for the 19 reversed samples is $D = 233.9$, $I = -48.0$, $k = 11.9$, $\alpha_{95} = 10.2$. These directions produce overlapping circles of confidence, so they are antipodal within confidence limits (Fig. 4). Inverting the reversed directions through the origin, the mean for both formations is $D = 57.2$, $I = 46.5$, $k = 13.1$, $\alpha_{95} = 8.0$ ($n = 27$). The mean declination suggests a clockwise tectonic rotation of about 47 ± 11° compared with the cratonic Oligocene pole of Diehl et al. (1983). Similar rotations have been reported from many other places in the Santa Monica Mountains and elsewhere in the western parts of the Transverse Ranges (Hornafius, 1985; Luyendyk et al., 1985; Luyendyk, 1991; Prothero et al., 1996). The mean inclination of 46.5 ± 11° is slightly shallower than the present inclination, suggesting a slight northward transport, but the error estimates are so large that the hypothesis of no translation cannot be ruled out.

Once the overprinting was removed and a stable component isolated, each direction was summarized by the least squares method of Kirschvink (1980) and averaged according to Fisher (1953) statistics. Each site was ranked according to the scheme of Opdyke et al. (1977). Of the 49 Orange County sites, 38 were statistically separated from a random distribution at the 95% confidence level (Class I sites of Opdyke et al., 1977). Six sites had fewer than three usable samples (usually because one sample crumbled before analysis), so site statistics could not be calculated (Class II sites of Opdyke et al., 1977). The remaining five sites showed a clear polarity preference in two samples, but the third sample was divergent (Class III sites of Opdyke et

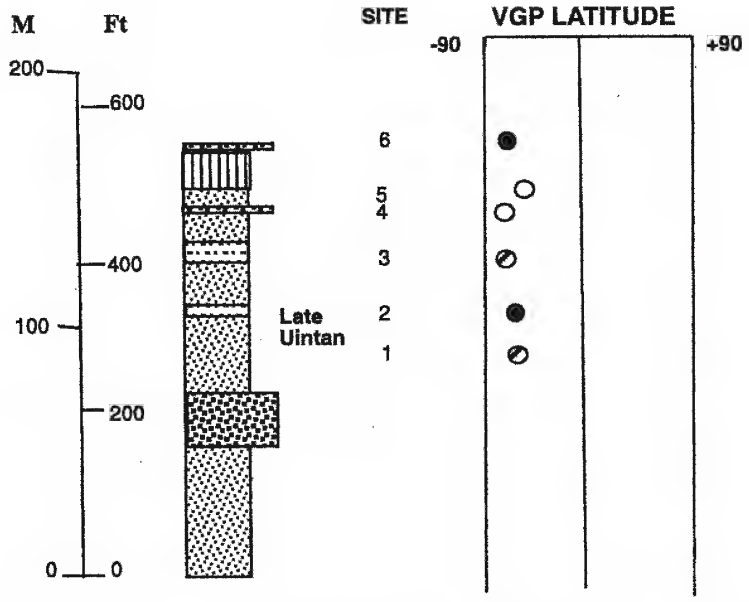

Figure 6 Lithostratigraphy and magnetic stratigraphy of the lower part of the Sespe Formation east of Highway 241 and north of the Windy Ridge Toll Plaza, Santa Ana Mountains, Orange County, California. Open circles are Class III sites, of which one site was divergent, but the other two gave a clear indication of polarity; all other symbols are as in Figure 5.

al., 1977). In the Piuma Road section in Los Angeles County, 17 sites were Class I, three sites were Class II, and seven sites were Class III.

Jamboree Road

The magnetic stratigraphy of the lower part of the Sespe Formation that is exposed along Highway 261 just south of Jamboree Road is shown in Figure 5. This section is the downward continuation of the Hemingfordian age section that was published by Prothero and Donohoo (2001: fig. 5), and its latitude and longitude are 33.76239°N, 117.75916°W. The lower 95 m of section is composed of 3–4-m-thick grayish red siltstone beds that are interbedded with tan sandstone beds. Above this interval are 53 m of grayish orange, matrix-supported to clast-supported conglomerate beds. The remainder of the section is dominated by massive sandstone beds.

All but two magnetic sites are statistically significant, and all are of reversed polarity. The lower 120 m of the section contained a late Uintan aggregate fauna (see Lander, 2002c; Calvano et al., 2003a, 2003b; Whistler and Lander, 2003) that includes such taxa as *Peradectes californicus* Stock, 1936; *Sespedectes singularis* Stock, 1935; *Dyseolemur pacificus* Stock, 1934; *Microparamys woodi* (Wood, 1959); *Pareumys* sp.; *Griphomys alecer* Wilson, 1940; *Simimys simplex* Wilson, 1949; and *Leptoreodon* Wortman, 1898. These assemblages are comparable to those that have been found in the Tapo Canyon and Brea Canyon local faunas, which were obtained from the middle member of the Sespe Formation in Simi Valley (Lander, 2002c).

According to Prothero et al. (1996), the late Uintan age Brea Canyon and Tapo Canyon local faunas are assignable to Chron C18r (40.0–41.1 Ma). Thus, we correlate the lower Sespe Formation exposures near Jamboree Road with Chron C18r. A large unconformity must lie somewhere near the top of this section (Fig. 11) because the succeeding strata are early Hemingfordian in age (no older than 19 Ma, according to Prothero and Donohoo [2001]).

Windy Ridge

This section is a thick badlands exposure on the east side of Highway 241 at the base of the grade just north of the Windy Ridge toll plaza on Highway 241; its latitude and longitude are 33.84481°N, 117.71665°W (Fig. 6). In this section, the Sespe Formation unconformably overlies the middle Eocene age Santiago Formation. A thick basal conglomerate is present, and above this conglomerate lies 45 m of 2 to 8-m-thick maroon siltstone beds interbedded with 14 to 28-m-thick light gray sandstone beds. Directly above these beds are 12 m of pale red sandstone and conglomerate beds with an irregular lower contact. This upper unit dips 6° more steeply

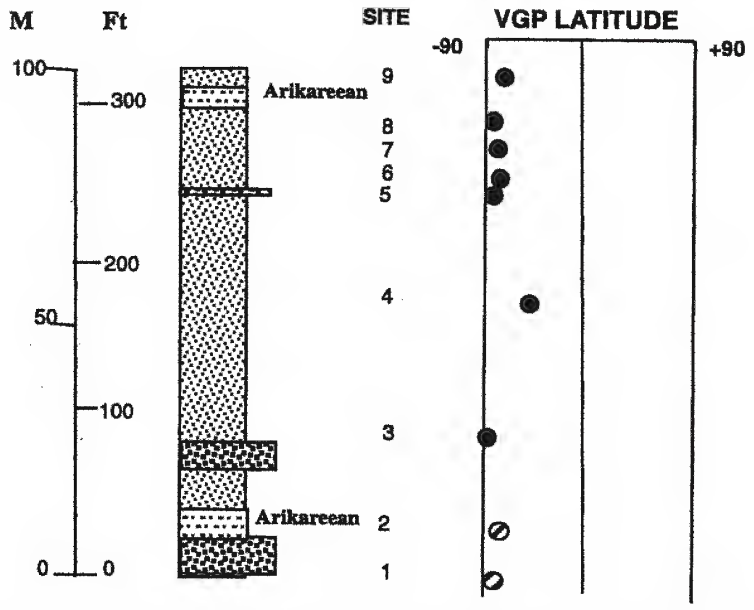

Figure 7 Lithostratigraphy and magnetic stratigraphy of the Sespe Formation along the northeast shore of Irvine Lake, Santa Ana Mountains, Orange County, California. Symbols are as in Figure 5.

than the underlying beds, indicating the presence of a disconformity between them.

Spanning about 165 m, the entire sampled part of the Windy Ridge section is reversed in polarity (the base was inaccessible). The red siltstone layers have produced a late Uintan correlative assemblage that includes *Sespedectes* sp. and *Simimys* sp. (Lander, 2002c; Calvano et al., 2003a, 2003b; Ludtke et al., 2003a, 2003b; Whistler and Lander, 2003). On the basis of the similarities of this assemblage with the late Uintan age Brea Canyon and Tapo Canyon local faunas, which are assignable to Chron C18r (40.0–41.1 Ma), we correlate the lower part of the Sespe Formation exposures near Jamboree Road with Chron C18r (Fig. 11).

Irvine Lake

A third sequence occurs along the northeastern shoreline of Irvine Lake (Fig. 7), where an area of badlands exposures contains fossil mammals. The latitude and longitude of this locality is 33.78001°N, 117.71594°W. In this exposed section, the Sespe Formation overlies the middle Eocene age Santiago Formation with apparent conformity. The formational contact is defined as a color change from yellow-orange to pale red sandstone. At the base of the section is a 10-m-thick bed of matrix-supported conglomerate. Above this conglomerate is a fossiliferous, 3-m-thick pale red siltstone bed. Approximately 32 m of moderately reddish brown conglomerate and sandstone overlie the siltstone bed. Above the latter interval is a 25-m-thick, very pale orange, poorly sorted, coarse-grained sandstone interval with rare maroon siltstone beds and conglomerate beds. The next 20 m of section includes interbedded 3 to 5-m-thick reddish brown siltstone beds and 4 to 8-m-thick, medium yellow-orange, coarse-grained sandstone beds.

This section is almost 100 m thick, and all but two of the nine sites are statistically significant and reversed in polarity. The top and bottom of the section produced Arikareean age land mammals such as *Proheteromys* sp. and *Trogomys* sp. (Calvano et al., 2003a, 2003b; Ludtke et al., 2003a, 2003b; Whistler and Lander, 2003), so we correlate it with Chron C10r (Fig. 11) on the basis of faunal similarities with the upper parts of the Sespe Formation in the Simi Valley (Prothero et al., 1996).

Santiago Canyon Road

This section occurs on the south side of Highway 241, just east of its intersection with Santiago Canyon Road; the latitude and longitude are 33.78673°N, 117.74342°W (Fig. 8). This sequence is more than 250 m thick, and the lower 108 m of the section consists of 4 to 5-m-thick grayish red siltstone beds that are interbedded with 1 to 24-m-thick pale orange sandstone beds. Overlying this interval is 41 m of orange to pink and pale reddish brown sandstone and conglomerate beds. The base of this unit has a 3- to 5-cm-thick siltstone drape. Overlying this unit are 17 m of very pale orange, matrix-supported conglomerate with some sandstone and siltstone beds. The

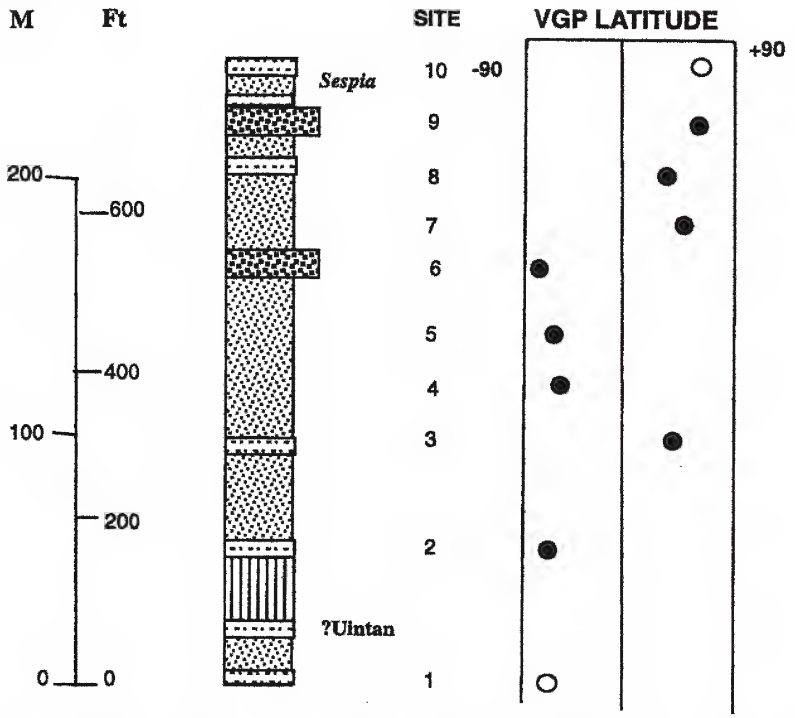

Figure 8 Lithostratigraphy and magnetic stratigraphy of the Sespe Formation along the south side of Highway 241 on the east side of Santiago Road, Orange County, California. Symbols are as in Figures 5 and 6.

upper 70 m of the section consists of 15 to 26-m-thick, very pale orange sandstone and conglomeratic sandstone beds interbedded with 1 to 2-m-thick reddish brown siltstone beds.

All but two of the 10 magnetic sites in this stratigraphic section are statistically significant. The lowest part of the section contained a late Uintan age assemblage, including the rodent *Simimys* sp. (Lander, 2002c; Calvano et al., 2003a, 2003b; Whistler and Lander, 2003), so we correlate it with Chron C18r. The remaining normal–reversed–normal part of the section seems to be associated with the upper part of the sequence. At the top of the section is an early Arikareean age fauna that includes the oreodont *Sespia californica* Stock, 1930, and the rodents *Trogomys, Proheteromys,* and *Miospermophilus* (Lander et al., 2001a; Lander, 2002c; Calvano et al., 2003a, 2003b; Whistler and Lander, 2003). In the Simi Valley, *Sespia*-bearing beds are correlated with Chron C9r–C10r (28.0–29.4 Ma, according to Prothero et al., 1996). The Santiago Road normal–reversed–normal sequence probably correlates with Chrons C10n–C11n (28.4–30.0 Ma) because *Sespia californica* first occurs in Chron C10r in Simi Valley (Prothero et al., 1996). These data indicate that there is an unconformity in the section spanning the interval from 40.0 to 29.4 Ma (Fig. 11).

Laguna Hills

A fifth section occurs in the northern Laguna Hills (latitude and longitude = 33.63589°N, 117.76712°W), where earthmoving for a housing project resulted in numerous new exposures of the Vaqueros Formation and uncovered many marine fossils (Fig. 9). More than 170 m of section was sampled along the main ridge top exposures, and all but one of the 13 sites is statistically significant. The basal 30 m of the section has reversed polarity; the upper part of the section is normal.

Just north of this section, an isolated dip slope covered with a dense coquina of *Turritella inezana* also was sampled. Although this sequence was only about 10 m thick, both of its sites (Laguna Canyon sites 14 and 15; Table 1) are reversed in polarity. On the basis of a projection of these beds along strike, they probably correlate with the lower reversed section to the south (unless the two areas are separated from each other by faulting).

Correlation of these sections is much more difficult (Fig. 11). As pointed out above, the Vaquerosian molluscan stage spans the late Oligocene and early Miocene (from 17 to 28 Ma in age), so the mollusks are not sufficiently age-diagnostic for refined correlation (Prothero

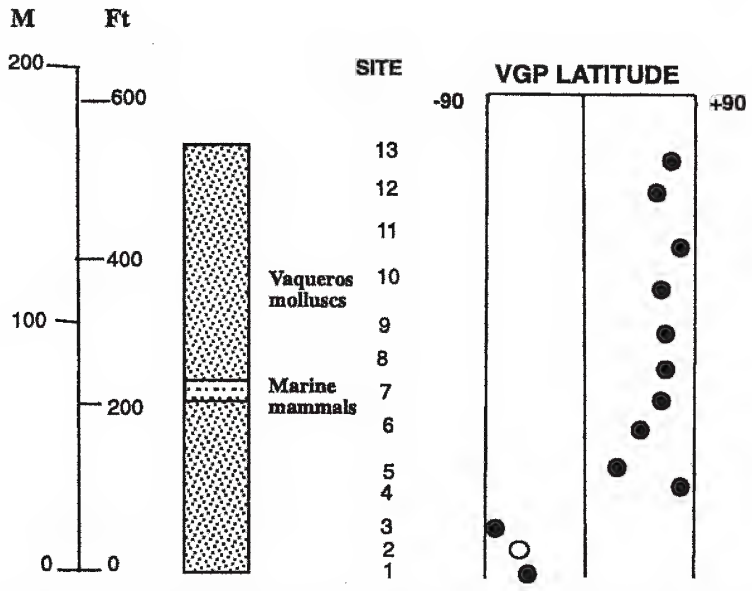

Figure 9 Lithostratigraphy and magnetic stratigraphy of the Vaqueros Formation in the northern Laguna Canyon area, Orange County, California. Symbols are as in Figures 5 and 6.

and Donohoo, 2001; Prothero and Hoffman, 2001). The marine mammal fauna is comparable to several other latest Oligocene and early Miocene faunas in North America, but because the late Oligocene and early Miocene have many polarity changes, this is not very helpful. The best correlation is with Chrons C5Dn–C5Dr or C5En–C5Er on the basis of the occurrence of early Hemingfordian mammals in the underlying Sespe redbeds (Prothero and Donohoo, 2001).

Piuma Road

A sixth section, which spans over 500 m, was sampled along Piuma Road, beginning 0.3 miles (0.5 km) east of its intersection with Saddle Peak Road in the Santa Monica Mountains of Los Angeles County (Fig. 10). These sites have latitude 34°4′9″ to 34°4′12″N and longitude 118°39′37″ to 118°40′4″W. The lower 86 m of the section spans the lower Piuma Member of the Sespe Formation. This interval consists of thick red and tan sandstones that have yielded the early Arikareean rodent *Leidymys nematodon* (Cope, 1881) and the marsupial *Herpetotherium* Cope, 1873 (Fisk et al., 2001; Lander et al., 2001a, 2001b), at LACM locality 7345 (19 m above the base of the section). Mammal and frog bone fragments occur elsewhere within this interval. Very near the top of this unit occurs the Lower Saddle Peak Tuff, which has been $^{40}Ar/^{39}Ar$ dated at 27.2 ± 0.2 Ma (Lander et al., 2003) and confirms that the underlying land mammal assemblage is early Arikareean. Above the lower part of the Piuma Member of the Sespe Formation is an 18-m-thick sequence of gray marine sandstone of the Carbon Canyon tongue of the Vaqueros Formation, which yields the early Vaquerosian mollusk *Turritella inezana bicarina* Loel and Corey, 1932, myliobatid ray tooth fragments, *Sabalites* (Lesquereux, 1878) palm fronds, and petrified log impressions. This Vaqueros sequence apparently interfingers with the Sespe Formation because, above the tongue, lies more than 1,000 m of the upper Piuma Member of the Sespe Formation. At the base of the upper part of the Piuma Member is the upper Saddle Peak Tuff, which has been $^{40}Ar/^{39}Ar$ dated at 21.1 ± 0.2 Ma (Lander et al., 2003). Above the ash is a 50-m-thick covered interval. The remainder of the upper part of the Piuma Member is exposed sporadically in a westerly direction along Piuma Road. At the 427–428-m level in the section are LACM localities 7329 and 7330, which have produced an early Hemingfordian correlative fauna containing ochotonid lagomorphs and the rodents *Yatkolamys* Martin and Corner, 1980, and *Trogomys* sp. (Fisk et al., 2001; Lander et al., 2001a, 2001b). Unconformably overlying the Sespe Formation exposures is the middle Miocene age Saddle Peak Member of the Topanga Canyon Formation, which consists of a thick basal conglomerate that has a dense coquina of the late Vaquerosian age scallop *Vertipecten bowersi* (Arnold, 1906) at the base (as mapped by Dibblee, 1993). Two sites were sampled in this interval, but the lack of additional exposures and the limited scope of this

Table 1 Site statistics. **ABBREVIATIONS**: n, number of samples; D, declination (°); I, inclination (°); k, precision parameter; α_{95}, ellipse of 95% confidence interval.

Site	n	D	I	k	α_{95}
Irvine Lake					
1	1	198.8	−17.8	—	—
2	1	182.9	−57.5	—	—
3	3	183.9	−45.7	12.0	37.3
4	3	121.4	−67.7	16.4	31.5
5	3	178.4	−49.4	6.9	51.0
6	3	163.2	−52.4	5.9	56.2
7	3	163.6	−58.6	15.4	32.6
8	3	187.4	−59.4	13.5	35.0
9	3	166.5	−33.9	14.8	33.3
Reversed mean	21	169.2	−53.8	10.2	10.5
Windy Ridge					
1	2	214.6	−64.0	39.7	40.7
2	3	159.0	−37.9	11.8	37.6
3	2	166.4	−43.6	441.7	11.9
4	3	183.2	−60.1	4.7	64.4
5	2	145.3	−30.9	3.8	180.0
6	3	169.2	−64.6	10.4	40.4
Reversed mean	15	168.2	−52.7	8.2	14.2
Laguna Canyon					
1	3	139.0	−24.2	15.6	32.3
2	3	210.6	−29.3	3.5	78.8
3	3	187.2	−52.0	26.7	24.3
4	3	7.7	54.5	7.2	49.9
5	3	67.9	33.7	13.9	34.4
6	3	47.8	51.7	14.3	33.9
7	3	15.1	36.1	12.3	36.8
8	3	356.2	32.5	6.9	51.1
9	3	14.7	40.1	77.8	14.1
10	3	4.6	68.2	34.9	21.2
11	3	4.4	61.4	18.4	29.6
12	3	11.8	69.0	46.2	18.4
13	3	350.9	38.9	12.1	37.2
14	2	155.6	−52.9	6.4	127.7
15	2	208.3	−55.8	32.4	45.4
Reversed mean	13	177.6	−45.6	5.6	19.2
Normal mean	30	16.7	51.3	9.0	9.3
Jamboree Road					
1	3	199.5	−55.8	11.3	38.6
2	3	192.1	−70.5	39.3	19.9
3	3	178.9	−56.5	16.6	31.2
4	3	165.1	−56.2	18.3	29.7
5	3	158.0	−53.5	15.9	32.0
6	2	193.3	−67.0	77.4	28.8
7	3	177.8	−50.3	42.8	19.1
8	3	182.7	−78.6	49.8	17.7
9	1	156.0	−19.4	—	—
10	3	179.2	−69.1	79.8	13.9
11	3	174.2	−53.2	10.6	40.0
Reversed mean	29	178.2	−61.5	20.0	6.1
Santiago Road					
1	3	177.3	−31.1	4.7	64.6
2	2	148.8	−22.2	38.0	41.7
3	3	49.7	17.9	11.2	38.7
4	3	143.5	−47.0	13.0	35.7

Table 1 Continued.

Site	*n*	*D*	*I*	*k*	α_{95}
5	3	165.3	−18.3	8.9	44.1
6	3	174.3	−45.3	14.3	33.9
7	3	17.4	21.7	21.8	27.1
8	3	43.5	64.5	6.2	54.2
9	3	9.3	36.7	5.3	59.9
10	3	342.2	49.0	4.9	63.1
Reversed mean	14	162.7	−34.3	8.8	14.2
Normal mean	15	21.4	39.7	5.3	18.4
Formational means, Orange County					
Reversed samples	94	171.3	−52.4	9.2	5.1
Normal samples	45	18.4	47.7	7.3	8.5
Entire formation	139	0.5	51.6	7.9	4.6
Piuma Road, Los Angeles County					
1	3	220.9	−59.8	3.7	76.5
2	3	82.7	69.7	32.7	21.9
3	3	62.8	58.8	9.3	42.9
4	3	248.4	44.5	18.3	29.7
5	3	221.7	27.7	6.8	51.3
6	2	59.8	31.7	101.0	25.1
7	3	238.1	−28.4	7.4	48.8
8	3	246.2	−42.8	11.7	37.7
9	3	237.0	−46.1	8.2	46.3
10	3	55.3	49.5	6.6	52.4
11	3	52.1	54.2	16.6	31.3
12	3	81.7	22.9	46.9	18.2
13	3	65.6	23.5	20.9	27.7
14	2	236.6	−52.2	5.8	143.2
15	3	244.5	−31.5	3.5	80.2
16	3	301.6	−26.0	4.9	62.9
17	3	285.7	−43.4	6.3	53.8
18	3	245.1	−44.5	15.6	32.4
19	3	218.9	−53.9	4.5	66.7
20	3	167.5	−36.5	4.6	65.6
21	3	223.3	−57.5	3.7	76.2
22	3	199.9	−57.3	5.7	57.5
23	3	217.3	−52.9	2.6	102.8
24	2	220.9	−38.1	5.1	180.0
25	3	198.3	−43.1	19.0	29.1
26	3	252.5	−49.8	5.7	57.4
27	3	56.9	28.2	25.9	24.7
Formational means, Los Angeles County					
Reversed samples	19	233.9	−48.0	11.9	10.2
Normal samples	8	64.2	42.7	17.2	13.8
Entire formation	27	57.2	46.5	13.1	8.0

study did not permit further sampling of the Topanga Canyon Formation.

Twenty-seven magnetic sites spanning the entire 500 m of the section were sampled at suitable outcrops. Seventeen sites were Class I, three sites were Class II, and seven sites were Class III (Fig. 10). The basal portion of the lower part of the Piuma Member is reversed in polarity, and it is succeeded by a normal interval (that contains early Arikareean age land mammals), which is in turn succeeded by another reversed interval that continues up-section into the Vaqueros Formation exposures, and includes the $^{40}Ar/^{39}Ar$ date of 27.2 ± 0.2 Ma. The remaining Vaqueros Formation interval is normal in polarity. The entire upper part of the Piuma Member of the Sespe Formation is reversed in polarity (except for the basal 50-m-thick covered interval, whose polarity is indeterminate), and includes the $^{40}Ar/^{39}Ar$ date of 21.1 ± 0.2 Ma from very near its base. The two sites at the base of the Topanga Canyon Formation were reversed (lower

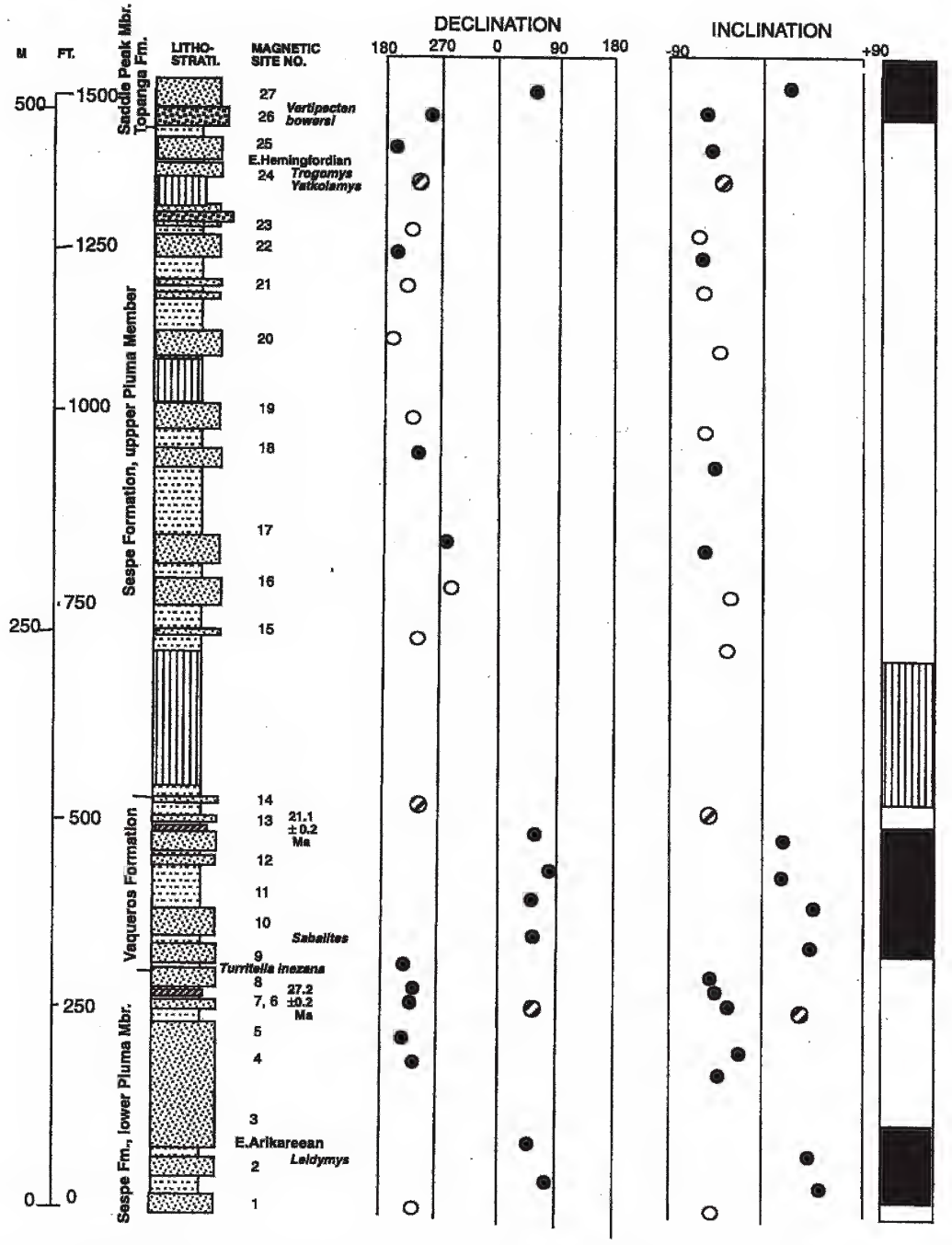

Figure 10 Lithostratigraphy, biostratigraphy, and magnetic stratigraphy of the Sespe and Vaqueros formations along Piuma Road, Santa Monica Mountains, Los Angeles County, California. Symbols are as in Figures 5 and 6. Original declination and inclination are used, rather than virtual geomagnetic pole (VGP) latitude as in previous figures, because sites are tectonically rotated.

site) in polarity, then normal (upper site) in polarity.

Correlation with the magnetic polarity timescale is shown in Figure 11. The $^{40}Ar/^{39}Ar$ date of 27.2 ± 0.2 Ma and the presence of early Arikareean correlative land mammals calibrate the lower part of the section (lower Piuma Member of the Sespe Formation and the Carbon

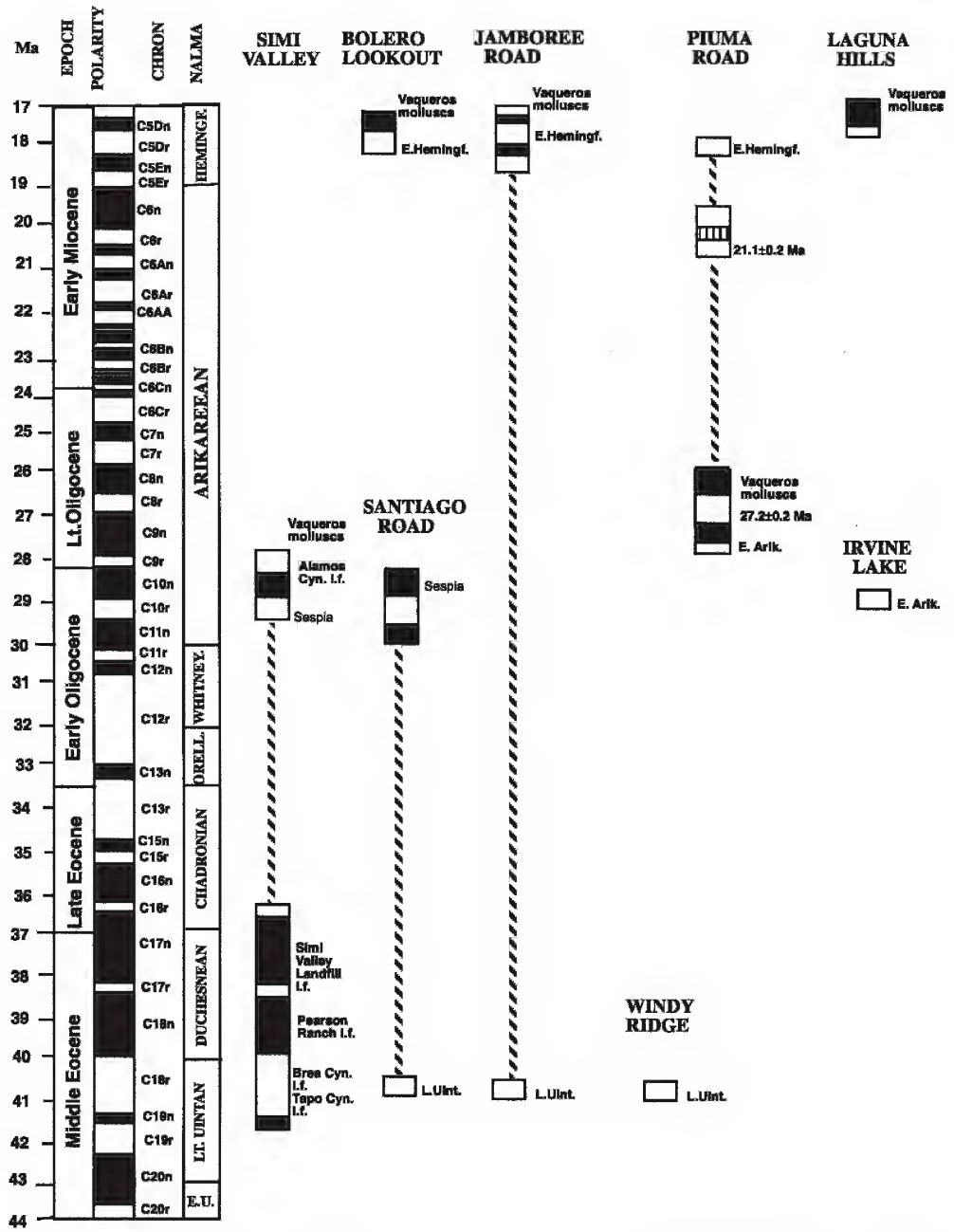

Figure 11 Probable correlations of the Sespe and Vaqueros formations to the global and local timescale (following Prothero et al. [1996] and Berggren et al. [1995]). Magnetostratigraphy of the Sespe Formation in the Simi Valley area, Ventura County, California, based on Prothero et al. (1996); Bolero Lookout and upper Jamboree Road sections of Orange County, California, based on Prothero and Donohoo (2001).

Canyon tongue of the Vaqueros Formation) with Chrons C8n–C9r (26.0–28.2 Ma). It is likely that there is a long unconformity between the two tuffs, because only 60 m of section represent the 6.1 million years separating the two dates. It is also possible that some of the missing section has been removed by a fault that intersects Piuma Road between the two tuffs. The long reversed interval in the upper part of the Piuma Member is more difficult to calibrate. The $^{40}Ar/^{39}Ar$ date of 21.1 ± 0.2 Ma suggests that the base of the sequence correlates with Chron C6Ar (21.2–

21.9 Ma), but the early Hemingfordian land mammals at the top of the member suggest that the upper reversed sequence correlates with Chron C5Er (18.6–18.9 Ma) at the oldest (and possibly younger). The section does not appear to record normal Chrons C6n, C6A1n, or C6A2n. Possibly one or more of them is missing in the covered interval between sites 14 and 15 (Fig. 10), or there is at least one undetected major unconformity in this interval. If so, the lower part of the upper Piuma Member correlates only with Chron C6Ar, and the upper part correlates with Chron C5Er (Fig. 11). Such cryptic unconformities already are documented elsewhere in southern California (see above), so they would be expected to be encountered in the Santa Monica Mountains as well.

DISCUSSION

Correlations of the sections that were studied for this paper are summarized in Figure 11. As shown in that figure, three stratigraphic sections (Santiago Canyon Road, Windy Ridge, and the Simi Valley sections of Prothero et al. [1996]) have reversed magnetozones that correlate with Chron C18r on the basis of their late Uintan correlative land mammals. The Santiago Canyon Road section contains early Arikareean age or younger mammals at the top of the sequence. Therefore, the upper part of the section is much younger than the base, and there is a major unconformity in the section.

This unconformity is regional, being documented in the Sespe Formation wherever it is exposed (Prothero et al., 1996), and it documents the removal of the entire sequence of strata of late Eocene and early Oligocene age, an interval of at least 7 million years. In the Orange County exposures, there are no Duchesnean age mammals, so the unconformity there represents the interval from approximately 30 to 40 Ma, or at least 10 million years. In some places, however, the unconformity appears to represent even more time, such as where the early Hemingfordian mammals overlie late Uintan mammals in the Jamboree Road section. Here, the unconformity represents the interval from 19 to 40 Ma, or about 21 million years.

In the Windy Ridge, Santiago Canyon Road, and Irvine Lake sections, the unconformity lies at the base of an interval containing pale red sandstone and conglomerate beds. This relationship was noted as well by Howard (1988) in the Santa Ynez Mountains of Santa Barbara County. In the Jamboree Road section, the thick conglomerate beds in the middle of the section represent a dramatic shift to a higher energy environment. Therefore, the base of the conglomerate beds is the most likely location of the unconformity in this area. The lower part of the Sespe Formation, where it is present, is composed of strata deposited in a meandering fluvial environment. The unconformity progressively cuts out more section to the southeast, and there apparently is no lower part of the Sespe Formation in the area southeast of Irvine Lake. More biostratigraphic research in the area is necessary to document this possibility.

Figure 11 gives the impression that the middle Cenozoic stratigraphic record in California is much less complete than previously supposed. Early authors (e.g., Stock, 1948) depicted the Santiago Sespe and Vaqueros sequence as if it were one continuous sequence spanning most of Eocene, Oligocene, and early Miocene time. However, the precise calibration of individual sections shows that deposition of the Sespe and Vaqueros sequence took place during several limited time intervals, primarily from 37 to 41 Ma, 28 to 30 Ma, and 17 to 21 Ma. The only exception is the Las Posas Hills section in Ventura County, which contains the Kew Quarry Local Fauna (see Tedford et al., 2004:173) of possibly late Whitneyan age (Lander, 1994a, 1994b, 1997, 2002a; Prothero et al., 1996), although other authors are not convinced of this and assign it to the early Arikareean (see discussion in Prothero et al., 1996). The geochronologic intervals from 21 to 28 Ma and 30 to 37 Ma are completely unrepresented by any strata in the region. In some places, such as in the Jamboree Road section, the unconformity appears to span the entire interval from 19 to 41 Ma (equal to the entire late Eocene, Oligocene, and earliest Miocene). This is consistent with Ager's (1963) observation that the stratigraphic record is actually "more gaps than record" and similar to the pattern that has been reported for Cenozoic marine rocks of the Pacific Coast of the United States (Prothero, 2001).

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Paleomagnetism of the Oligocene and Miocene Lincoln Creek and Astoria formations, Knappton, Washington

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ABSTRACT. The upper Oligocene Lincoln Creek Formation and the lower Miocene Astoria Formation, exposed on the north bank of the Columbia River near Knappton, Washington, have long been important localities for marine fossils. Oriented magnetic samples were taken at low tide from 12 sites spanning the exposed parts of both formations and analyzed by both thermal and alternating field demagnetization. The characteristic remanence was held primarily in magnetite, with minor amounts of goethite overprinting. Both reversed and normal polarities were obtained, and they passed a reversal test for stability. The rocks show a mean direction of $D = 67.2$, $I = 62.5$, $k = 5.8$, $\alpha_{95} = 11.3$, which suggests almost 77 ± 11 degrees of clockwise tectonic rotation, consistent with other results reported for the region, but they show no significant latitudinal translation. The lower part of the Lincoln Creek Formation is reversed in polarity, followed by a short normal magnetozone. The contact between the two formations is covered, but the available exposures of the Astoria Formation are entirely reversed in polarity. On the basis of the presence of late Oligocene molluscan faunas (*Liracassis apta* Zone) and correlation with the magnetic stratigraphy of the Lincoln Creek Formation at Canyon River on the south flank of the Olympic Mountains, we correlate the Knappton section of the Lincoln Creek Formation with either Chrons C7Ar–C6Cn2r (25.7–23.3 Ma) or C7r–C6Cn2r (25.4–23.3 Ma). The age of the Astoria reversed magnetozone is poorly constrained, and it could be as young as 20 Ma (million years before present). The locations of key fossil horizons within this stratigraphic sequence are discussed.

INTRODUCTION

Fossiliferous rocks of the Lincoln Creek and Astoria formations near the now-defunct cement plant and sawmill at the abandoned town site of Knappton, Washington, are exposed at low tide on the north bank of the Columbia River, across from Astoria, Oregon (Fig. 1). They were first mapped by Weaver (1937), later mapped in more detail by Wells (1979, 1989), and described further by Moore (1984a). According to Moore (1984a), several different fossiliferous levels are within the Lincoln Creek sequence. The lowest, Unit I (LACMIP 5844; Natural History Museum of Los Angeles County, Department of Invertebrate Paleontology), contains abundant gooseneck barnacles, which were described by Zullo (1982). Unit II (LACMIP 5843) contains many decapod crustaceans (not yet described). Unit III (LACMIP 5852) contains glass sponges described by Rigby and Jenkins (1983). Unit IV (LACMIP 5842) is known as the *Aturia* bed because of the abundance of the nautiloid *Aturia* (Bronn, 1838). Fossils from the Lincoln Creek Formation near Knappton have also been illustrated, described, or both in a number of other reports (e.g., Rathbun, 1926; Miller, 1947; Moore, 1984b, 1988; Squires, 1989; Goedert and Squires, 1993; Squires and Goedert, 1994), as well as in a brief summary of the fish fossils by Welton (in Moore, 1984a:7).

In the overlying Astoria Formation are several LACM localities, including the type locality of the desmatophocine otarioid pinniped *Desmatophoca brachycephala* Barnes, 1987. Fossil crabs have also been reported from the Astoria Formation near Knappton (Berglund and Goedert, 1992; Schweitzer and Salva, 2000). Not only are the Knappton localities the source of many

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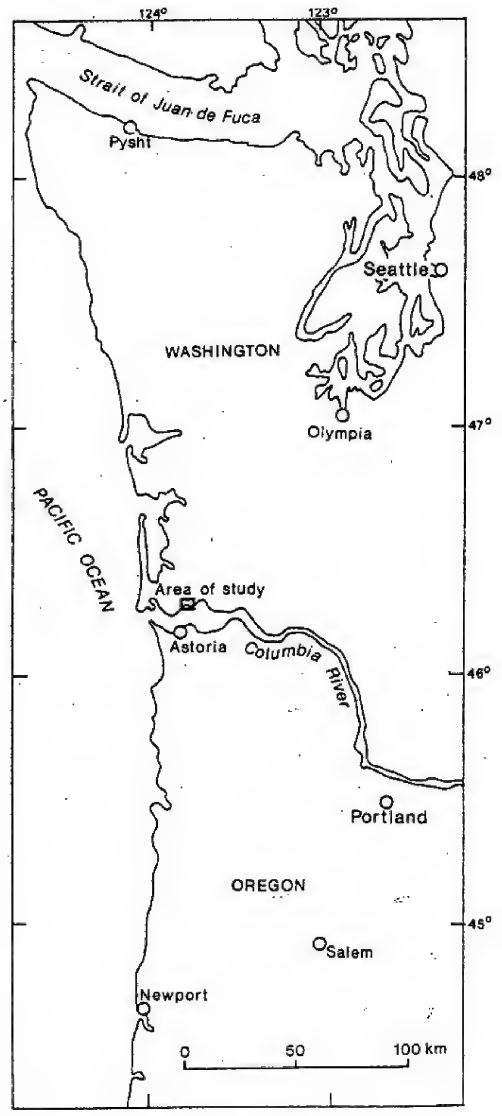

Figure 1 Index map showing location of Knappton and other localities that are mentioned in text in western Oregon and Washington.

important specimens in the LACM (Natural History Museum of Los Angeles County) collections, but they could also be of historical importance as well. Some of the first fossils from the West Coast of North America, collected by J.D. Dana with the Wilkes Exploring Expedition, might have been found in Knappton outcrops (Weaver, 1942:76).

However, the ages of these strata and fossils are still not well constrained. Zullo (1982) assigned the Lincoln Creek sequence to the upper Eocene and upper Oligocene. Rigby and Jenkins (1983) suggested the sequence ranges in age from late Eocene to middle Miocene. Moore (1984a) assigned the sequence to the upper part of the *Liracassis apta* Zone (Moore, 1984b, 1988) and suggested that it is earliest Miocene in age. She indicated that most of the mollusks belong to the Juanian Molluscan Stage (of Addicott, 1976a, 1976b), although the assemblage has strong resemblances to the overlying early Miocene Pillarian Stage. Squires and Goedert (1994) assigned the sequence a tentative age range of latest early Oligocene to earliest late Oligocene on the basis of the presence of specimens of *Liracassis* Moore, 1984b, that appear to be transitional between *Liracassis rex* (Tegland, 1931) and *L. apta* (Tegland, 1931).

In the last two decades, considerable progress has been made in dating the marine rocks of the Pacific Northwest. Through the use of planktonic microfossils and magnetic stratigraphy, most of the key sections have now been dated and correlated to the global timescale of Berggren et al. (1995). The longest, most complete section through the Lincoln Creek and Astoria formations, at Canyon River on the southern Olympic Peninsula of Washington, was studied by Prothero and Armentrout (1985). The type section of the Juanian Molluscan Stage in the Pysht Formation (Durham, 1944) was studied by Prothero et al. (2001c), and the type section of the Pillarian Stage in the Clallam Formation was studied by Prothero and Burns (2001). Correlative sections in the Yaquina Formation and Nye Mudstone in Oregon were studied by Prothero et al. (2001b), and in the overlying Astoria Formation by Prothero et al. (2001a). With the use of these sections as standards, it should now be possible to further refine the age of the Knappton localities with magnetic stratigraphy.

METHODS AND MATERIALS

The stratigraphic section follows the measurements of George Moore (personal communication) and the descriptions and photographs in Moore (1984a). A map of the localities is shown in Figure 2. Samples were collected during low tide in the summer of 2001 with the use of simple hand tools to recover oriented blocks of rock (three samples per site to obtain site statistics). Oriented cores were then drilled from the blocks with a drill press or prepared from smaller pieces of rock with Zircar aluminum oxide ceramic. The samples were measured on a 2G cryogenic magnetometer at the California Institute of Technology with the use of an automatic sample changer. After measurement of natural remanent magnetization (NRM), each sample was demagnetized in alternating fields (AFs) of 25, 50, and 100 gauss to determine the coercivity behavior (and magnetite content) of the samples and demagnetize any multidomain grains before their remanence was baked in. After AF demagnetiza-

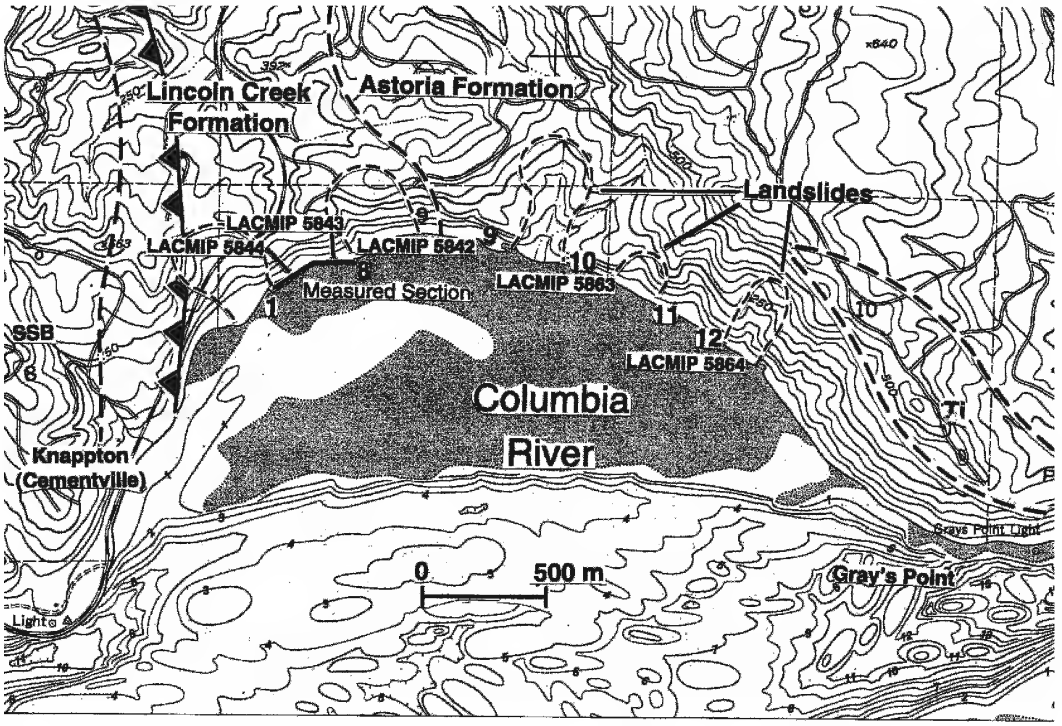

Figure 2 Detail of the topographic map of the Columbia River northern shoreline, showing the location of Moore's (1984a) LACMIP fossil localities and of our paleomagnetic sites. Map based on the United States Geological Survey Knappton, Oregon–Washington 7.5′ quadrangle, with geologic features after Wells (1979).

tion, each sample was then thermally demagnetized at 50°C steps from 200° to 600°C to remove any chemical remanence held by iron hydroxides such as goethite and to determine whether any remanence held by hematite remained after the Curie point of magnetite (580°C) had been exceeded.

About 0.1 g of powdered rock from several samples was subjected to increasing isothermal remanent magnetization (IRM) to determine their IRM acquisition behavior, and thus the relative abundance of magnetite or hematite They were also AF demagnetized twice: once after having acquired an IRM produced in a 100-mT (millitesla) peak field and once after having acquired an anhysteretic remanent magnetization (ARM) in a 100-mT oscillating field. Such data are useful in conducting a modified Lowrie–Fuller test (Pluhar et al., 1991), which indicates whether single or multidomain grains are present.

Fossils of taxa mentioned in the text are deposited in the collections of the LACM, the UWBM (Burke Museum of Natural History and Culture), or both.

ABBREVIATIONS

AF	Alternating fields
IRM	Isothermal remanent magnetization
LACM	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA
LACMIP	Natural History Museum of Los Angeles County, Department of Invertebrate Paleontology locality
NRM	Natural remanent magnetization
UWBM	Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington USA

RESULTS

Orthogonal demagnetization ("Zijderveld") plots of representative samples are shown in Figure 3. In most samples, there is a dramatic response to AF demagnetization, suggesting that the remanence is held largely in a low-coercivity mineral such as magnetite, although the slight decrease in magnetization in the first AF steps suggests a minor overprinting by an iron hydroxide such as goethite. The abrupt decrease in intensity at 200°C (above the dehydration temperature of goethite) suggests the removal of a high-coercivity remanence held in iron hydroxides. In a few samples (e.g., Fig. 3C), thermal demagnetization at 200°C removed a slight overprint to reveal a stable reversed direction. In nearly every sample,

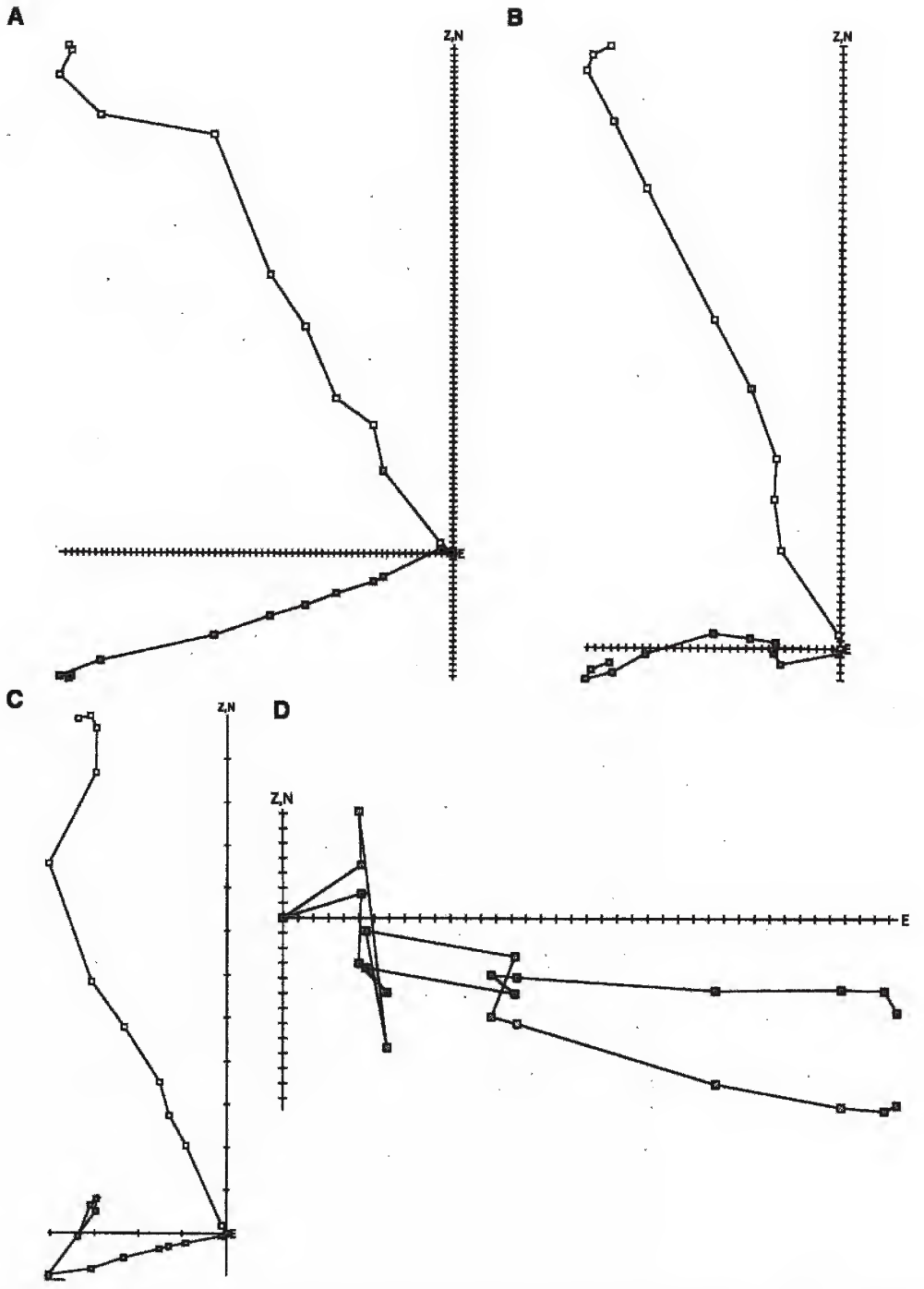

Figure 3 Orthogonal demagnetization plots of representative samples from the Lincoln Creek and Astoria formations (tilt-corrected). Solid squares indicate horizontal component; open squares indicate vertical component. First four AF steps are NRM, 25, 50, and 100 gauss, followed by thermal steps of 200, 300, 350, 400, 450, 500, 550, and 600°C. Each division = 10^{-6} emu.

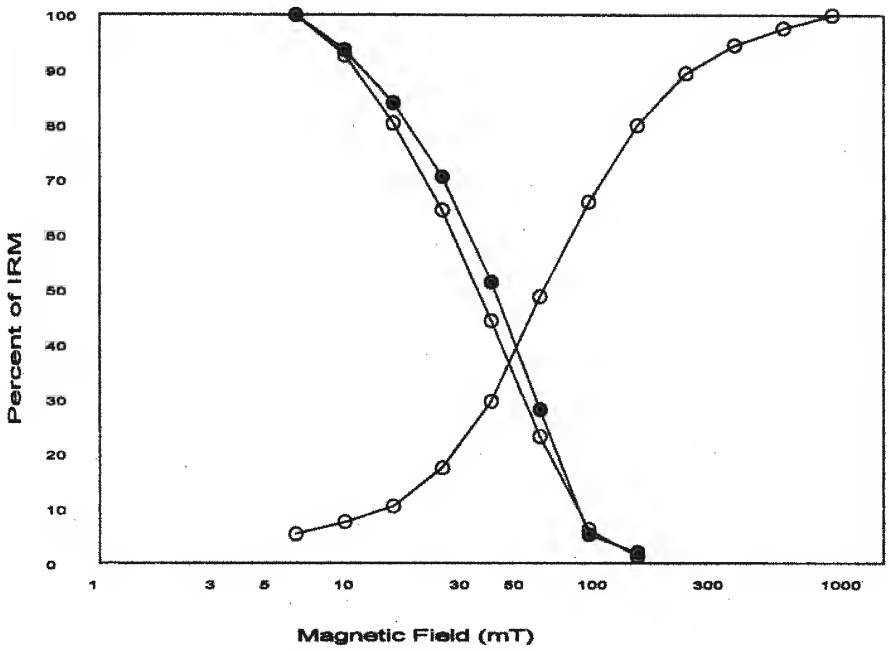

Figure 4 IRM acquisition (ascending curve on right) and Lowrie–Fuller test (two descending curves on left) of representative powdered samples from the Lincoln Creek and Astoria formations. Open circles = IRM; solid circles = ARM.

the remanence was completely gone by 500°C, which is more consistent with a mineral such as magnetite, which has a Curie temperature of 580°C. Thus, it seems likely that the remanence is held mainly in magnetite, with minor chemical overprinting by goethite or other iron hydroxides.

Representative IRM acquisition analyses are shown in Figure 4. Most samples showed near saturation at 300 mT, suggesting that the remanence is held largely in magnetite, although the continuing increase in IRM suggests some hematite was present as well. In most samples, the ARM was more resistant to AF demagnetization than the IRM, suggesting that the remanence is held in single-domain or pseudo–single-domain grains.

Most of the samples showed a direction pointed southwest and up at NRM and showed only a single component of magnetization, which decayed steadily to the origin (Fig. 3A and 3B). Because these data are dip-corrected, this is clearly a reversed direction that has undergone clockwise rotation. A few samples (Fig. 3C) had a slight overprint but showed the characteristic reversed and rotated direction by 300°C. Two sites (Fig. 3D) pointed east and down from NRM to 600°C, which is a normal direction with clockwise rotation. Thus, it is apparent that the direction is a primary or characteristic remanence and not an overprint or later magnetic component.

This is confirmed by the reversal test (Fig. 5). The mean for the five normal samples was D =

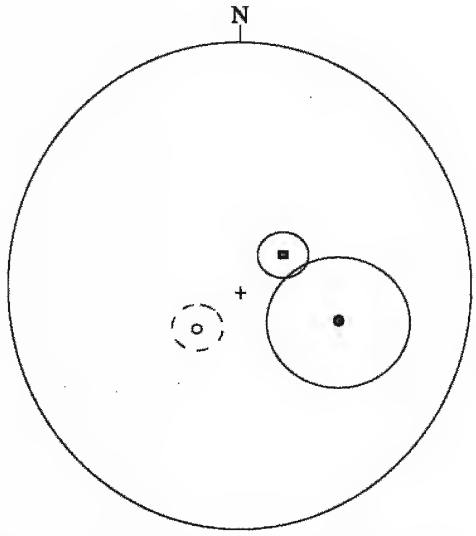

Figure 5 Stereoplot of mean poles and circles of confidence for the data discussed in this study. Solid circles indicate lower hemisphere projections; dashed lines and open circles indicate upper hemisphere projections. Solid square indicates mean of reversed samples projected through the origin to the lower hemisphere.

Table 1 Site statistics. **ABBREVIATIONS:** n = number of samples; D = declination (°); I = inclination (°); k = precision parameter; α_{95} = ellipse of 95% confidence interval.

Site	n	D	I	k	α_{95}
1	2	182.0	−35.2	13.9	73.0
2	3	249.4	−74.9	111.4	11.7
3	3	238.5	−56.8	10.4	40.3
4	3	203.2	−59.0	2.3	113.0
5	3	213.6	−47.4	4.8	64.0
6	3	208.5	−68.1	7.9	47.2
7	2	101.0	24.8	208.0	17.4
8	3	115.2	48.5	42.4	19.2
9	3	222.6	−71.0	6.1	54.8
10	3	295.4	−70.3	24.3	25.6
11	3	230.5	−61.5	13.4	35.1
12	3	243.7	−44.4	3.0	90.8
Normal samples	5	108.4	39.2	22.7	16.4
Reversed samples	30	233.7	−64.4	6.1	11.8
Formational mean	35	67.2	62.5	5.8	11.3

108.4, I = 39.2, k = 22.7, α_{95} = 16.4; the mean for the 30 reversed samples was D = 233.7, I = −64.4, k = 6.1, α_{95} = 11.8. These directions, although not directly opposite one another, show overlapping circles of confidence, so they are antipodal within confidence limits (Fig. 5). Clearly, these directions are primary or characteristic directions, and not modern normal overprints, in that they are largely reversed and show a rotation consistent with that seen elsewhere in this area in rocks of this age. Inverting the reversed directions through the origin, the mean for the formation was D = 67.2, I = 62.5, k = 5.8, α_{95} = 11.3.

Once the overprinting had been removed and a stable component was isolated, each direction was summarized by the least squares method of Kirschvink (1980) and averaged with Fisher (1953) statistics (Table 1). Each site was then ranked according to the scheme of Opdyke et al. (1977). Of the 12 sites, seven were statistically separated from a random distribution at the 95% confidence level (Class I sites of Opdyke et al., 1977). Two sites had only two usable samples, so no site statistics could be calculated (Class II sites of Opdyke et al., 1977). The remaining three sites showed a clear polarity preference, but the third sample was divergent (Class III sites of Opdyke et al., 1977).

The magnetic polarity stratigraphy is shown in Figure 6. The lower 100 m of the sampled section of the Lincoln Creek Formation is entirely reversed in polarity, including sites containing the gooseneck barnacle bed (Unit I of Moore, 1984a; = LACMIP 5844) and the decapod crustacean bed (Unit II of Moore, 1984a; = LACMIP 5843). The next 70 m of section are normal in polarity. The interval from 250 m to approximately 500 m in the section was covered by landslides, so it could not be sampled for paleomagnetic analysis. It includes the *Aturia* locality (Unit IV; = LACMIP 5842). From 500 m to more than 600 m in the section, the exposed outcrop of Astoria Formation is entirely reversed in polarity, including localities LACMIP 5863 and LACMIP 5864 and the type locality of the desmatophocine otarioid pinniped *Desmatophoca brachycephala* Barnes, 1987.

DISCUSSION

A tentative correlation of this stratigraphic section with the global timescale of Berggren et al. (1995) and the Pacific Coast timescale of Prothero (2001) is shown in Figure 7. The presence of *Liracassis apta* and other Juanian Stage mollusks places the Lincoln Creek part of the section in the late Oligocene, and Moore (1984a) indicated that some of the other mollusks suggest affinities with those of the early Miocene Pillarian Stage, so she argued that the Knappton Lincoln Creek molluscan fauna is late Juanian in age. In the Canyon River section of the Lincoln Creek and Astoria formations (Prothero and Armentrout, 1985), the *L. apta* (Moore, 1984b) Zone (and Juanian Stage) spans magnetic Chrons C10n–C6Cr; this is also true of the type Juanian section in the Pysht Formation (Prothero et al., 2001c). Thus, the best correlation of the long reversed interval followed by the short normal magnetozone of the Knappton Lincoln Creek section is either Chrons C7r–C7n, or C7Ar–C7An (Fig. 7).

The long talus-covered interval stratigraphically higher than site 8 (Fig. 6) makes the remaining correlations less certain. It could potentially obscure several magnetic polarity changes, so when the reversed section of the Astoria Formation is encountered, it is difficult to decide which of the many reversed early Miocene intervals best correlate with it. If the covered interval is a long one, or if the section has hidden unconformities, this reversed interval of Astoria Formation could correlate with

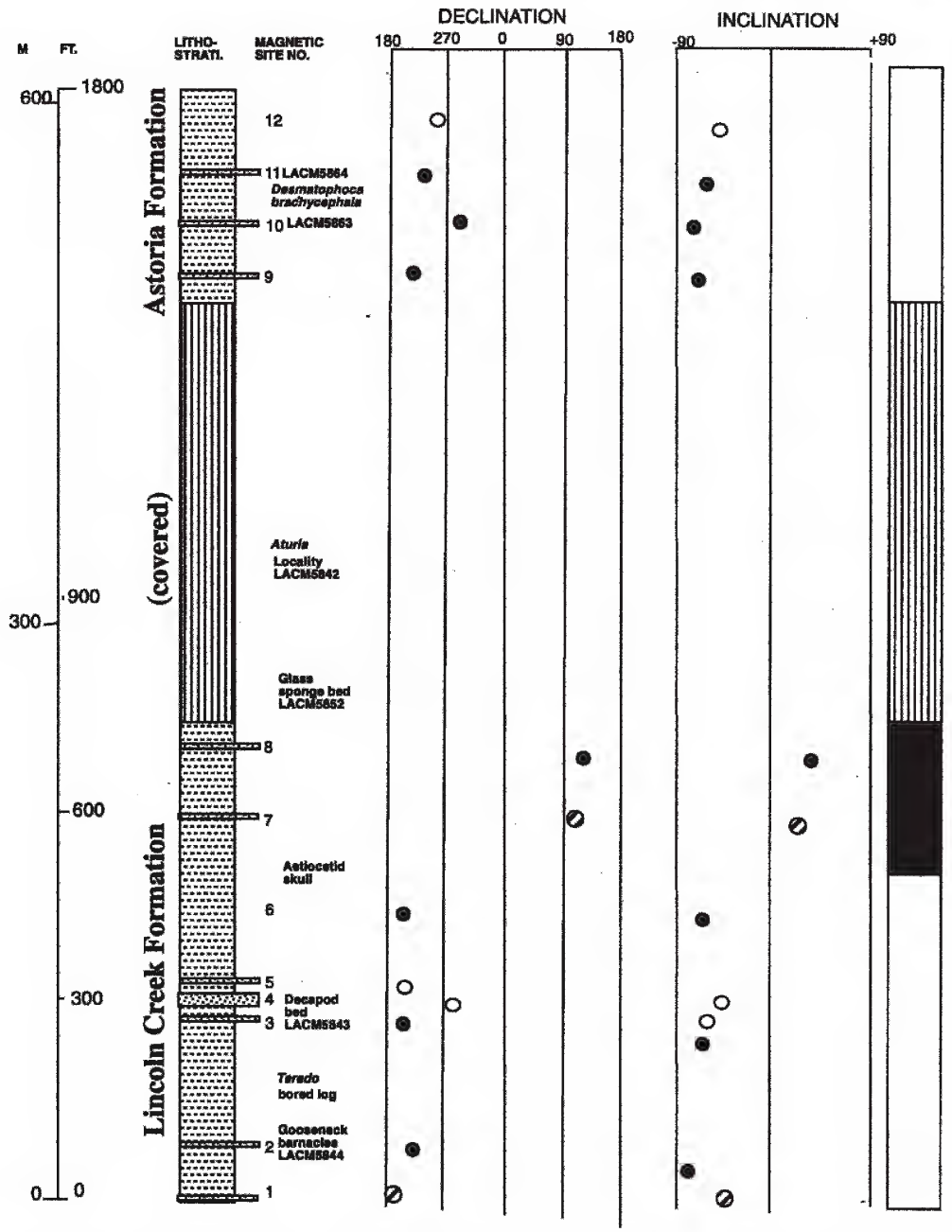

Figure 6 Lithostratigraphy and magnetic stratigraphy of the Lincoln Creek and Astoria formations (stratigraphy after G.W. Moore [personal communication] and Moore [1984a]). LACMIP fossil localities of Moore (1984a) indicated. Solid circles indicate Class I sites (following Opdyke et al., 1977), which are statistically distinct from a random distribution at the 95% confidence level; circles with diagonal slash pattern are Class II sites, in which one sample was missing, so site statistics could not be calculated; open circles are Class III sites, in which one site was divergent, but the other two gave a clear indication of polarity.

Astoria beds as young as C5Br (15–16 Ma), as shown by magnetostratigraphic analysis of the Astoria Formation in the Newport, Oregon, area (Prothero et al., 2001a). However, several specimens of *Aturia angustata* Conrad, 1848, have been found at LACMIP 5863 (encompassing our sites 9 and 10), low in the Astoria Formation. According to Moore and Moore (2002) this nautiloid became

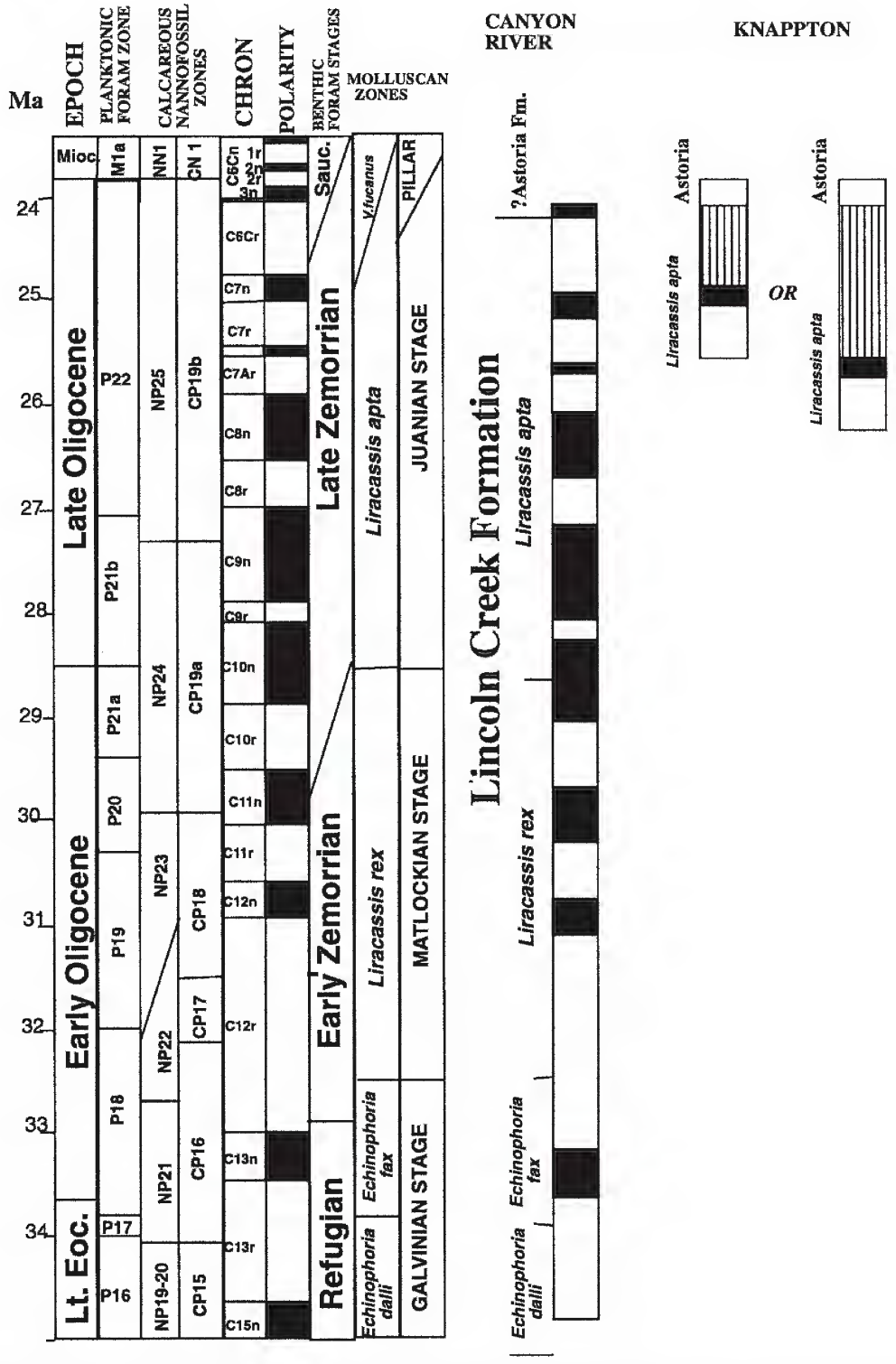

Figure 7 Two possible correlations of the Lincoln Creek and Astoria formations at Knappton to the global and local timescale (following Prothero [2001] and Berggren et al. [1995]), and to the magnetostratigraphy of the Lincoln Creek and Astoria formations at Canyon River (after Prothero and Armentrout, 1985).

extinct approximately 17 Ma, so we know that sites 9 and 10 are at least that old. Furthermore, fragments of the pectinid bivalve *Vertipecten fucanus* (Dall, 1909), a zonal mollusk for the Pillarian Stage (Addicott 1976a, 1981), have also been found at LACMIP 5863. Farther east, and higher in the Astoria Formation, LACMIP 5864 (encompassing our sites 11 and 12) marks the stratigraphically lowest occurrence, locally, of the gastropod *Fulgoraria* (*Miopleiona*) *indurata* (Conrad, 1849). According to Addicott (1976a) this would also mark the lower boundary of the Pillarian Stage, although it also occurs in the middle Miocene Newportian Stage.

On the basis of correlations with the type Pillarian section in the Clallam Formation (Prothero and Burns, 2001), we suggest that the Astoria Formation east of Knappton best corresponds to one of the reversed intervals in Chron C6C: C6C1r, C6C2r, or later reversed intervals. We suggest that the Knappton section of the uppermost Lincoln Creek and Astoria formations is temporally equivalent to at least the lower part of the original (and now concealed) type section of the Astoria Formation, approximately 10 km to the south, in the city of Astoria, Oregon. It is significant that Dall and Harris (1892) divided the exposures of the Astoria Formation at Astoria, Oregon, into three stratigraphically successive members (Astoria shale, *Aturia* bed, and Astoria sandstone), and this would apply equally well to the section that is exposed at Knappton, Washington. Additionally, Addicott (1976a, 1976c) and Moore and Addicott (1987) referred the lower part of the original type section of the Astoria Formation to the Pillarian Stage. On the basis of correlations with the type section of the Pillarian Stage in the Clallam Formation (Prothero and Burns, 2001), we suggest that the Lincoln Creek and Astoria formations section at Knappton best corresponds to one of the reversed intervals in Chron CBC: CBC1r, CBC2r, or later reversed intervals, We cannot precisely date the very top of the section, but we know that it must have an age between 15 and 23 Ma.

The mean direction $D = 67.2$, $I = 62.5$, $k = 5.8$, $\alpha_{95} = 11.3$ suggests about 77 ± 11 degrees of clockwise tectonic rotation compared with the Oligocene cratonic pole of Diehl et al. (1983) and corrected according to Demarest (1983). The nearest basement rock, the Eocene Crescent Volcanics Domain 7 (of Wells and Coe, 1985; Table 1), has a clockwise rotation of 65 ± 17°, and is thus statistically indistinguishable from our results. South of Knappton, in northern Oregon, rotations of 74 ± 5° were found in the upper Eocene–lower Oligocene Keasey Formation (Prothero and Hankins, 2000) and of 72 ± 11° in the lower Oligocene Pittsburg Bluff Formation (Prothero and Hankins, 2001). Thus, our rotational results are consistent with those of similar age reported in the nearest studies to the north and south.

The mean inclination of 62.5 ± 11° suggests a paleolatitude of 46°, which is virtually identical to its present latitude of 46°17′N. Thus, there is no indication in these rocks of any significant northward translation since the early Miocene (as expected for such young rocks after the emplacement of most of the Cascades and their basement terranes).

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A new genus and species of Eocene protocetid archaeocete whale (Mammalia, Cetacea) from the Atlantic Coastal Plain

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ABSTRACT. *Crenatocetus rayi*, a new genus and species of fossil archaeocete whale from probable late middle Eocene Atlantic Coastal Plain deposits of the United States, is the fifth member of the cetacean family Protocetidae to be named from the Western Hemisphere. The holotype was probably derived from the Comfort Member of the Castle Hayne Formation of late middle Eocene age (Lutetian or Claibornian stage correlative) at the Martin Marietta New Bern Quarry at New Bern, Craven County, North Carolina. This archaeocete is a midsize protocetid, with an estimated cranial length of approximately 750 mm. It has a dorsoventrally deep dentary, apparently the primitive eutherian mammalian dental formula; labiolingually compressed cheek teeth, the posterior ones each having an anterior notch; a relatively large p4; crenulated enamel on all known teeth; and cuspate lingual and labial cingula on the premolars and molars. Its closest relatives are the similarly sized, apparently geochronologically older, and in most characters more primitive *Georgiacetus vogtlensis* from Georgia and the larger, and in most characters more derived, *Pappocetus lugardi* from the Ombialla District, Nigeria. We erect the new protocetid subfamily, the Pappocetinae, to include these three species, which are united by having as shared characters closely spaced cheek teeth that have crowns with densely crenulate enamel and cuspate labial and lingual cingula. The enigmatic North American *Pontobasileus tuberculatus* belongs to the subfamily Pappocetinae. This species was overlooked in other publications about protocetid archaeocetes, possibly because it had been considered by some authors to be a Miocene odontocete. Its holotype is the anterior part of the trigonid of a two-rooted right p4, and it has the distinctive crenulate enamel and prominent cuspate cingula that are characteristic of pappocetines, but its enamel is more rugosely crenulate than that of *G. vogtlensis*, *C. rayi*, or *P. lugardi*. The holotype of *P. tuberculatus* might have been found in Alabama, and its age is unknown, but it might be middle Eocene. The p4 of *P. tuberculatus* is larger than that of *C. rayi* and 50% wider, and the two taxa are distinct. The subfamily Pappocetinae is the geochronologically earliest known, exclusively non-Tethyan clade of archaeocetes, and its included species appear to have been fully marine, highly mobile protocetid cetaceans that had dispersed into at least the North Atlantic and South Atlantic realms.

INTRODUCTION

Extant cetaceans and related fossil taxa are classified in two suborders: the echolocating toothed whales, the Odontoceti (odontocetes), and the bulk-feeding, and ultimately baleen-bearing whales, the Mysticeti (mysticetes). Their predecessors, morphologically and chronologically, were the extinct suborder Archaeoceti (archaeocetes), which are the most primitive of all cetaceans. The Archaeoceti include the very primitive Pakicetidae and Ambulocetidae, which were amphibious quadrupedal cetaceans that are phylogenetically closely related to the ungulate ancestors of whales (Gingerich and Uhen, 1996b, 1998; Geisler, 2001; Gingerich et al., 2001b; Thewissen et al., 2001), as well as the more derived and fully marine members of the families Protocetidae and Basilosauridae (see Kellogg, 1936; Barnes and Mitchell, 1978; Gingerich and Russell, 1990; Gingerich et al., 1993; Fordyce and Barnes, 1994; Thewissen et al., 1994, 1996a; Fordyce et al., 1995; Gingerich and Uhen, 1996a).

The number of named archaeocetes has increased greatly since the comprehensive review of the suborder by Kellogg (1936), and the current taxonomic and morphologic diversity of the Archaeoceti is much greater than previously

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recognized (Thewissen, 1998). Despite the recent dramatic increase in our knowledge of the Archaeoceti, especially the early members, there is no current synthesis of the group. Kumar and Sahni (1986) described a new family of long-irostral archaeocetes, the Remingtonocetidae, reallocated some previously named species from India and Pakistan to different genera and suborders, and briefly discussed the distribution and relationships of archaeocetes. Thewissen et al. (1996b) recently offered a preliminary classification of primitive taxa, and his multiauthored synthesis (Thewissen, 1998) deals with a variety of subjects involving archaeocetes.

As presently recognized, the suborder Archaeoceti contains the families Pakicetidae, Ambulocetidae, Protocetidae, Remingtonocetidae, and Basilosauridae (Fordyce and Barnes, 1994; Thewissen et al., 1996b; Thewissen, 1998; Uhen, 1999, 2004). The middle Eocene freshwater-dwelling (see Thewissen et al., 1996c) members of the Pakicetidae are the most primitive of all whales, and they had functional hindlimbs and skulls with dentitions more similar to terrestrial ungulates than are those of more derived archaeocetes (Thewissen et al., 1996b; Thewissen, 1998). These whales had the typical cetacean supraorbital processes of the frontals, but they also had fully formed posterior limbs, long tails, and clearly were amphibious. Ambulocetid fossils are known from nearshore marine deposits, but analysis of oxygen isotope ratios in ambulocetid tooth enamel indicates that these early whales could metabolize only fresh water (Thewissen et al., 1996c).

The family Protocetidae were more aquatically adapted archaeocetes, fully marine in habit (Thewissen et al., 1996c), with the posterior limbs becoming less functional than in earlier forms (Hulburt, 1998). They are known from middle Eocene and possibly uppermost lower Eocene nearshore marine deposits in Egypt, Nigeria, India, Pakistan, and the southern United States (Kellogg, 1936; Thewissen et al., 1996a, 1996b; Bajpai and Thewissen, 1998).

Although in some regards more primitive than protocetids, members of the family Remingtonocetidae are long-snouted archaeocetes whose overall skull shape is reminiscent of gavials. In addition to long and relatively narrow snouts, they had long mandibular symphyses, widely spaced cheek teeth, and small eyes. Remingtonocetids are known only by a few fossils from middle Eocene deposits in western India and Pakistan (Kumar and Sahni, 1986; Gingerich et al., 1995; Bajpai and Thewissen, 1998).

The Basilosauridae (*sensu* Barnes and Mitchell, 1978; Uhen, 1996a) are the best known archaeocetes, with species known by relatively complete skeletons, and they have been found in upper Eocene deposits of the Fayum region of Egypt (Stromer, 1908; Kellogg, 1936; Gingerich and Uhen, 1996a), the Middle East (Zalmout et al., 2000), Pakistan (Gingerich et al., 1997), New Zealand (Köhler and Fordyce, 1997), and the East and Gulf Coastal Plains of the United States (Kellogg, 1936; Uhen and Gingerich, 2001). Barnes and Mitchell (1978) divided the family into the smaller and more conservatively built members of the subfamily Dorudontinae and the large-bodied members of the subfamily Basilosaurinae, which had elongate bodies owing to greatly elongated vertebral centra in the lumbar and caudal regions. The Basilosauridae were apparently pelagic and essentially cosmopolitan (Fordyce and Barnes, 1994), and they are the apparent sister group to the Neoceti, which includes the more derived mysticetes (Barnes and Sanders, 1996a, 1996b, 1996c) and odontocetes (Barnes, 1990; Goedert and Barnes, 1996).

In recent years there has been a dramatic increase in discoveries and descriptions of archaeocetes. Beginning in the 1970s, explorations in Pakistan and India brought to light new examples of primitive archaeocetes that had lived in and around the eastern part of the Tethys Seaway during the middle Eocene (Kumar and Sahni, 1986; Gingerich et al., 1993, 1994, 1995, 2001a; Thewissen et al., 1994; Zalmout et al., 2000). Thewissen et al. (1996b) reassigned some species that were previously classified in the family Protocetidae to the more primitive families Pakicetidae and Ambulocetidae. All of the most primitive cetacean fossils are from deposits around the margins of the ancient Tethys Seaway, and this is the most likely geographic site of origin of Cetacea (Gingerich and Russell, 1981; Thewissen, 1998).

More highly evolved protocetid archaeocetes have been found in the Western Hemisphere as well, although they are rarer. Kellogg (1936:242–243) identified a single vertebra from Texas as *Protocetus* sp., and this is the first supposed record of the family Protocetidae from the Western Hemisphere. With our current knowledge of archaeocete diversity; the recent recognition of the families Pakicetidae, Ambulocetidae, and Remingtonocetidae; and our lack of knowledge of the postcranial skeletons of most archaeocete species, Kellogg's generic identification, and even the familial allocation of this vertebra from Texas, must now be regarded as suspect. The specimen was, nonetheless, an early indication that very primitive cetaceans, possibly comparable to the primitive archaeocetes from India and Pakistan, existed in the western North Atlantic.

Several new taxa of primitive archaeocetes are represented by fossils from several localities in the southeastern United States. The protocetid *Natchitochia jonesi* Uhen, 1998 (also see Uhen, 1996b), was named on the basis of a postcranial skeleton from the middle Eocene Milams Member of the Cook Mountain Formation near Natchitoches, Louisiana. The protocetid *Geor-*

giacetus vogtlensis Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998, was described on the basis of a partial skeleton from the middle Eocene age "Blue Bluff unit" in Georgia (see also Petkewich and Lancaster, 1984; Hulbert and Petkewich, 1991; Hulbert, 1993, 1994, 1996; Hulbert et al., 1998). Albright (1996) reported some isolated protocetid teeth from the Santee Limestone of middle Eocene age in South Carolina, which were later identified by Uhen (1999:table 1) as *Georgiacetus* cf. *G. vogtlensis*. Uhen (1999) named the large protocetine protocetid *Eocetus wardii* Uhen, 1999, from the Comfort Member of the Castle Hayne Formation of middle Eocene age in North Carolina (see also Uhen, 2001). A very primitive protocetid, *Carolinacetus gingerichi* Geisler, Sanders, and Luo 2005 (see also Geisler et al., 1996), has been described on the basis of a partial skull, dentaries, and some postcranial bones from the Tupelo Bay Formation of late middle Eocene age in South Carolina.

The purpose of this study is to report the sixth protocetid to be named from deposits on the Atlantic Coastal Plain of the United States. We have previously made preliminary reports (McLeod and Barnes, 1990, 1991, 1996) about this specimen, which is apparently from New Bern, North Carolina, and it has been mentioned by other authors (e.g., Albright, 1996:519; Williams, 1998:15; Uhen, 1999:table 1). This new genus and species of protocetid archaeocete can be distinguished from all other named species on the basis of dental characters and from most named species on the basis of mandibular characters.

In addition to extending the geographic range of the family Protocetidae, this new cetacean helps in determining the polarity of characters of *Georgiacetus vogtlensis* from Georgia, in interpreting the morphology and relationships of the middle Eocene protocetid *Pappocetus lugardi* Andrews, 1920, from Africa, and in identifying the heretofore enigmatic *Pontobasileus tuberculatus* Leidy, 1873, from the southeastern United States. We are preparing a separate study of other specimens from other localities that appear to represent similar or related species, together with a detailed redescription of the holotype and referred specimen of *P. lugardi* (e.g., see McLeod and Barnes, 1990, 1991, 1996).

A cladistic analysis is deferred because of the disparate parts representing the described taxa, rendering a phylogenetic analysis and the cladogram representing it as more subjective and less meaningful than it might appear. The phylogenetic analysis prepared by Geisler et al. (2005) included *Georgiacetus vogtlensis*, which was based on a relatively complete skeleton, but it did not include its close relative *Pappocetus lugardi*, which is known by two mandibles and some referred vertebrae.

METHODS AND MATERIALS

The holotype of the new genus and species was found in a concretion of calcareous mudstone, from which it was prepared with the use of manual techniques and acid dissolution of the surrounding rock. Figure 3 contains reconstructions of partial dentaries that were created by combining the morphologies of both left and right sides to make the most complete composite restoration of the dentary possible.

ABBREVIATIONS

Specimens referred to here are in the collections of the following institutions, which are indicated by their associated abbreviations and so identified in the text.

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania USA
BM(NH)	Department of Paleontology, The Natural History Museum, London, Great Britain
ChM PV	Vertebrate Paleontology Collection, Department of Natural Sciences, The Charleston Museum, Charleston, South Carolina USA
GSM	Georgia Southern Museum, Georgia Southern University, Statesboro, Georgia USA
USNM	Department of Paleobiology, United States National Museum, Smithsonian Institution, Washington, D.C. USA

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Archaeoceti Flower, 1883

INCLUDED FAMILIES. Pakicetidae Gingerich and Russell, 1990 (Thewissen, Madar, and Hussain, 1996); Ambulocetidae Thewissen, Madar, and Hussain, 1996; Protocetidae Stromer, 1908; Remingtonocetidae Kumar and Sahni, 1986; and Basilosauridae Cope, 1868.

Family Protocetidae Stromer, 1908

INCLUDED SUBFAMILIES. Indocetinae Gingerich, Raza, Arif, Anwar, and Zhou, 1993; Protocetinae (Stromer, 1908) Gingerich and Russell, 1990; and Pappocetinae new subfamily.

Subfamily Pappocetinae new subfamily

DIAGNOSIS. A subfamily of Protocetidae differing from Indocetinae and Protocetinae by having a horizontal ramus of dentary deeper posteriorly; last premolar and all molars closely

spaced with no intervening diastemata; all teeth possessing pronounced crenulated enamel with rugose surface texture, in some areas forming irregular, apically directed ridges; cheek teeth possessing well-formed and prominent lingual and labial cingula that encircle bases of crowns; apices of crowns rounded and, additionally, on molars apically lobate.

TYPE GENUS. *Pappocetus* Andrews, 1920.

INCLUDED GENERA. *Crenatocetus* new genus; *Georgiacetus* Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998; *Pappocetus* Andrews, 1920; and *Pontobasileus* Leidy, 1873.

AGE AND DISTRIBUTION. Middle Eocene, eastern tropical Atlantic and western North Atlantic.

Crenatocetus new genus

"... a new species of protocetid archaeocete ..." McLeod and Barnes, 1990:35A.

"... a new protocetid archaeocete ..." McLeod and Barnes, 1991:46.

"A related taxon, a new genus and species ..." McLeod and Barnes, 1996:270.

"... unequivocal protocetid remains." Albright, 1996:519.

"Protocetid Whale of McLeod and Barnes." Williams, 1998:15.

"New Bern Protocetine." Uhen, 1999:table 1.

DIAGNOSIS OF GENUS. The diagnosis of the genus shall remain identical to that of the type species until additional species are described in the genus.

TYPE AND ONLY INCLUDED SPECIES. *Crenatocetus rayi* new species; type by designation.

AGE AND DISTRIBUTION. Middle Eocene (Lutetian to Bartonian or, in the southeastern United States, Claibornian age) or possibly early late Eocene (Bartonian to Priabonian or, in the southeastern United States, Jacksonian age), Atlantic Coastal Plain, United States.

ETYMOLOGY. The genus name is derived from *crena*, Latin for notch, in reference to the notch on the anterior side of the lower molar crowns and roots, and *cetus*, which is Latin for whale.

Crenatocetus rayi new species

Figures 1–3, 7A; Table 1

"... a new species of protocetid archaeocete ..." McLeod and Barnes, 1990:35A.

"... a new protocetid archaeocete ..." McLeod and Barnes, 1991:46.

"A related taxon, a new genus and species ..." McLeod and Barnes, 1996:270.

"... unequivocal protocetid remains." Albright, 1996:519.

"Protocetid Whale of McLeod and Barnes." Williams, 1998:15.

"New Bern Protocetine." Uhen, 1999:table 1.

DIAGNOSIS OF SPECIES. A species of medium-sized pappocetine protocetids, smaller as adults than *Pappocetus lugardi* and apparently than *Pontobasileus tuberculatus*, similar in size to *Georgiacetus vogtlensis*; differing from *P. lugardi* by having smaller adult body size, and having dentary with lateral side convex and bowed laterally rather than relatively flat, with large and ventrally deflected crest on ventral margin of the dentary posteriorly ventral to position of m3, anterior margin of mandibular foramen located posterior to level of m3 rather than immediately ventral to m3, proportionally wider p4 in anteroposterior dimension, p4 with posterolingual tubercle on the talonid, lingual cingula on p4 and m1–m3 nearly horizontal rather than arching at midpoint; differing from *G. vogtlensis* by having dentary with wider space between posterior edge of m3 and base of coronoid crest, more steeply ascending coronoid crest, relatively larger mandibular foramen, sulcus extending anteroventrally from margin of mandibular foramen, prominent ventrally flaring crest posteriorly ventral to mandibular foramen rather than smooth ventral margin, premolar and molar crowns more compressed labiolingually, with greater development of crenulations in enamel, and more prominent and more cuspate lingual and labial cingula that are proportionally approximately twice the dorsoventral height, and p4 relatively and absolutely larger but proportionally narrower labiolingually; differing from *P. tuberculatus* by having p4 crown more compressed labiolingually, and cheek tooth crowns with less rugosely crenulated enamel and less prominently cuspate lingual and labial cingula.

HOLOTYPE. USNM 392014, associated incomplete left and right dentaries with left p4 and broken m1–m3 and right posteriormost portion of p4, broken m1, lingual half of m2, and complete m3; collected by Danny G. Monk, obtained by USNM on 1 February 1985.

TYPE LOCALITY. Apparently the Martin Marietta Company's New Bern Quarry at New Bern, Craven County, North Carolina, USA (see discussion under "Formation and Age").

FORMATION AND AGE. The holotype was found in a concretion by Mr. Danny G. Monk of Atlantic Beach, North Carolina, in a truck load of marine "marl" that was being transported and used to fill a lot at Emerald Isle, North Carolina. Mr. Monk reported that the truck driver delivering the marl said that the fill had come from the Martin Marietta Belgrade Quarry, which is at Belgrade, Onslow County, North Carolina. This information seems to be incorrect, however, on the basis of geologic data. The rock unit that was being excavated for fill at the Belgrade Quarry is the marine upper Oligocene River Bend Formation (see Ward et al., 1978).

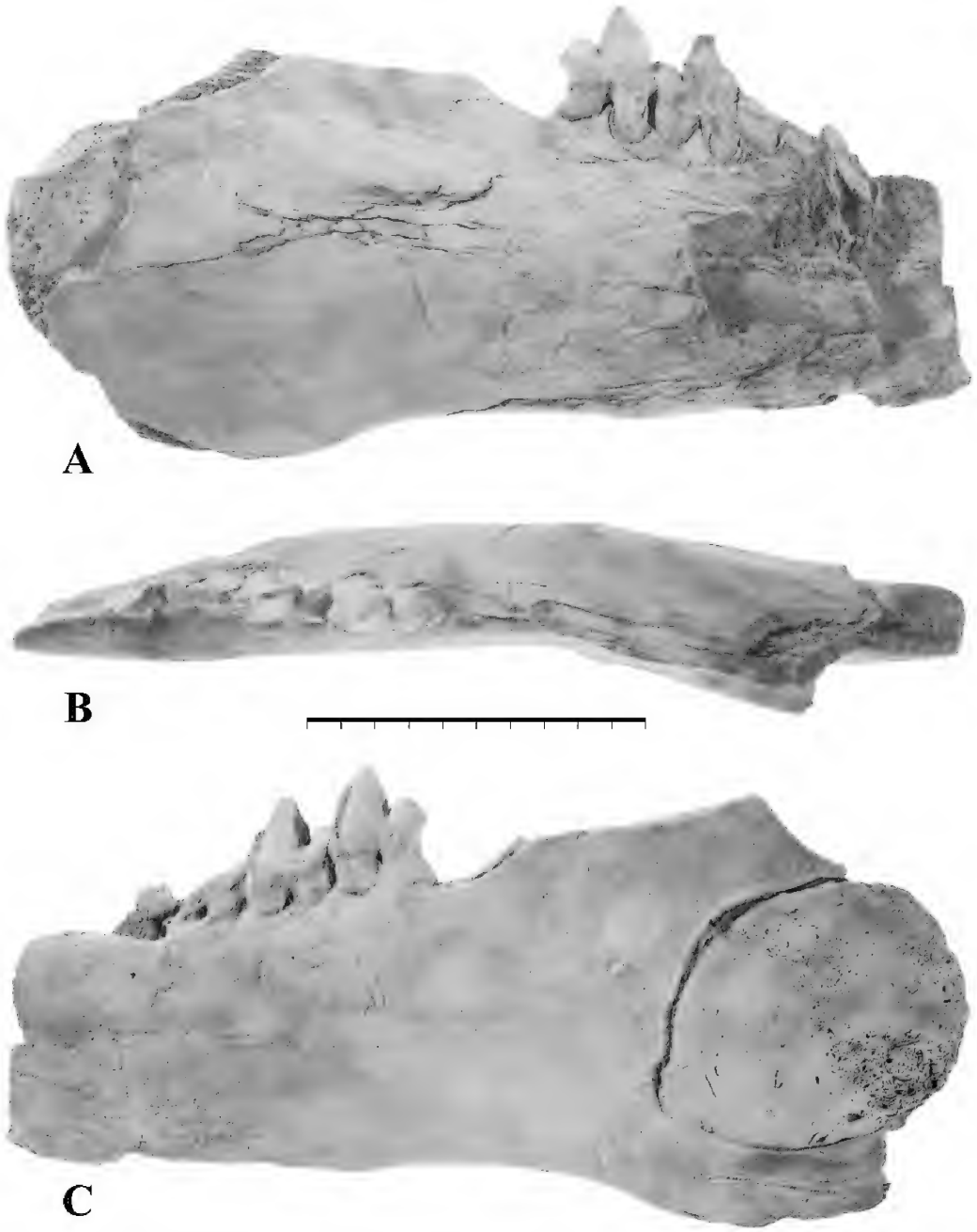

Figure 1 *Crenatocetus rayi* new genus and new species, holotype, USNM 392014, incomplete right dentary with posteriormost portion of p4, broken m1, lingual half of m2, and complete m3: **A,** labial view; **B,** occlusal view; **C,** lingual view. Scale bar = 10 cm.

No protocetids have been reported from any deposits younger in age than middle Eocene (see Fordyce and Barnes, 1994; Hulbert et al., 1998), and it is therefore very unlikely that the holotype of *Crenatocetus rayi* was derived from upper Oligocene deposits such as the River Bend Formation.

A more likely explanation is that the load of rock in which the specimen was discovered had originated at another quarry in North Carolina

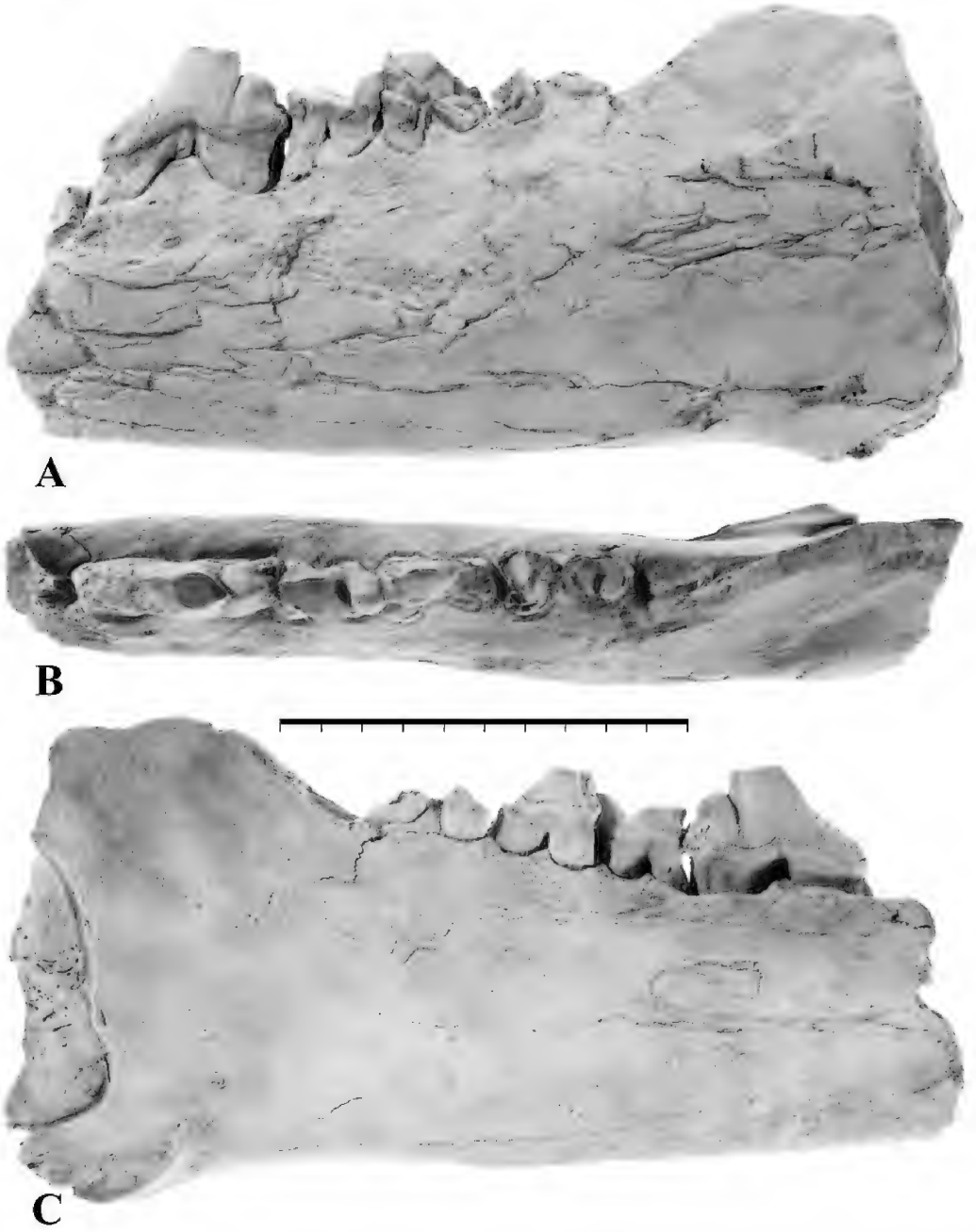

Figure 2 *Crenatocetus rayi* new genus and new species, holotype, USNM 392014, incomplete left dentary with p4 and broken m1–m3: **A,** labial view; **B,** occlusal view; **C,** lingual view. Scale bar = 10 cm.

where a middle Eocene deposit was being excavated for fill by the Martin Marietta Company. Just such a site is the New Bern Quarry, which was being operated at the same time by the Martin Marietta Company at New Bern in Craven County, North Carolina.

At the New Bern Quarry, the Eocene Castle Hayne Formation is exposed, and it consists of three members: the lower New Hanover Member, the middle Comfort Member, and the upper Spring Garden Member (see Ward et al., 1978). It is unclear whether the rock unit that overlies the Castle Hayne Formation at the New Bern Quarry is the River Bend Formation of middle to late Oligocene age (as reported by Ward et al., 1978), or the New Bern Formation of late Eocene age (as

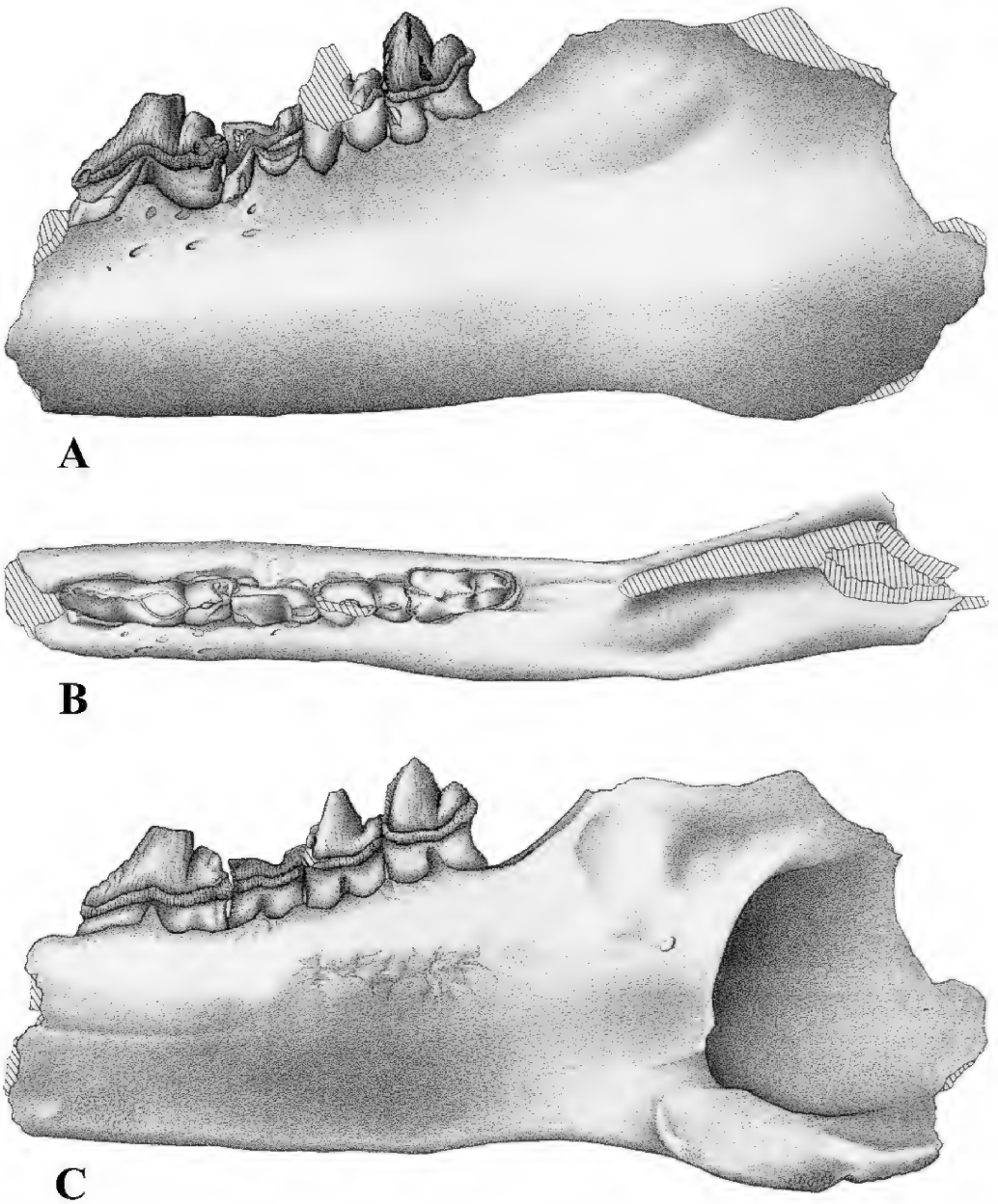

Figure 3 *Crenatocetus rayi* new genus and new species, reconstruction of dentary and teeth based on composite of both right and left dentaries of holotype, USNM 392014: **A**, labial view of left dentary; **B**, occlusal view of left dentary; **C**, lingual view of right dentary.

reported by Baum et al., 1978).There are disagreements about the ages of these deposits. Ward et al. (1978) listed the Comfort and Spring Garden Members of the Castle Hayne Formation as Gosport age (late middle Eocene, upper Claibornian correlative), whereas Harris and Zullo (1980) extended the Castle Hayne Formation well up into the Jacksonian Stage (= late Eocene). Baum et al. (1978) regarded the New Bern Formation as Jacksonian (= late Eocene) in age, but Harris and Zullo (1980) restricted it to the uppermost Jacksonian (= latest Eocene).

Lauck Ward of the United States Geological Survey examined a sample of the rock matrix that was attached to the holotype of *Crenatocetus rayi* and determined that it lacks the common predominant mollusks of the middle Spring Garden Member of the Castle Hayne Formation

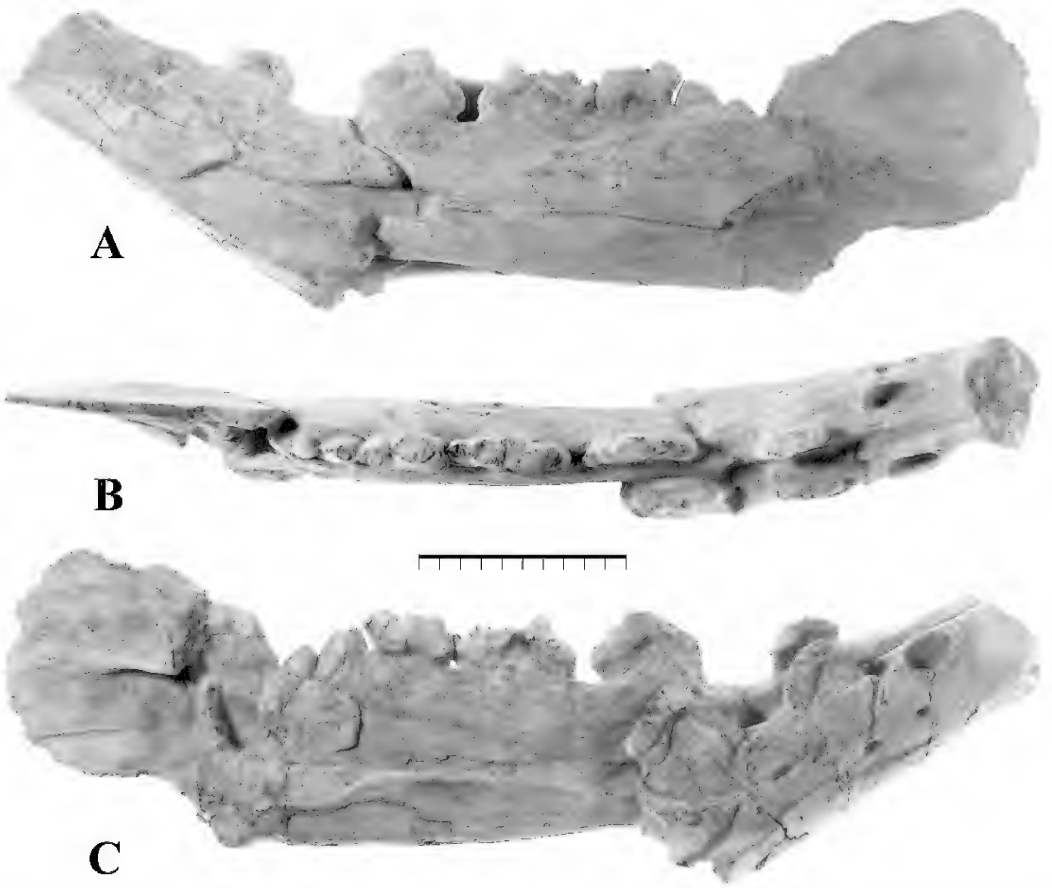

Figure 4 *Pappocetus lugardi* Andrews, 1920, holotype, BM(NH) M-11414, incomplete mandible, consisting of parts of both the right and left dentaries: **A,** labial view of left dentary; **B,** occlusal view of articulated right and left dentaries; **C,** labial view of right dentary with lingual surface of left dentary. Scale bar = 10 cm.

(R. Purdy, USNM, personal communication). Because of its grade of evolution, it is not likely that the holotype of *C. rayi* came from the older, basal New Hanover Member of the Castle Hayne Formation, and it is more likely that it could have originated from the upper Comfort Member of that formation.

On the basis of anecdotal discovery information, the matrix that was adhering to the holotype, and the stage of evolution of the taxon, the most likely source of the holotype of *Crenatocetus rayi* is the Comfort Member of the Castle Hayne Formation of upper middle Eocene age at the Martin Marietta Company's New Bern Quarry in Craven County, North Carolina.

ETYMOLOGY. The species is named in honor of Dr. Clayton E. Ray, formerly curator of Paleobiology at the USNM, who has greatly contributed to, fostered, and supported the study of fossil marine mammals, and who invited us to study this specimen.

DESCRIPTION. The holotype (Figs. 1–3) consists of the middle portions of associated left and right dentaries of one adult individual. The left dentary retains a small portion of the posterior root of p3, a complete p4, the m1 minus most of its trigonid cusp, the m2 with all of its labial face broken away, and the roots of the m3. The preserved part of the left dentary extends from the level of the posterior root of the p3 to just past the beginning of the medial lamina of the mandibular foramen, but the dorsal portion of the coronoid process and the ventral and posterior portions of the angular process are missing. The preserved part of the right dentary extends from about the level of the p4 to an area approximately just anterior to the mandibular condyle. Most of the mandibular foramen and the angular process are present, but the coronoid process is mostly lost. A substantial portion of the posterior root of the p4 is present, along with a posterolingual portion of the talonid cusp. Only a posterolingual portion of

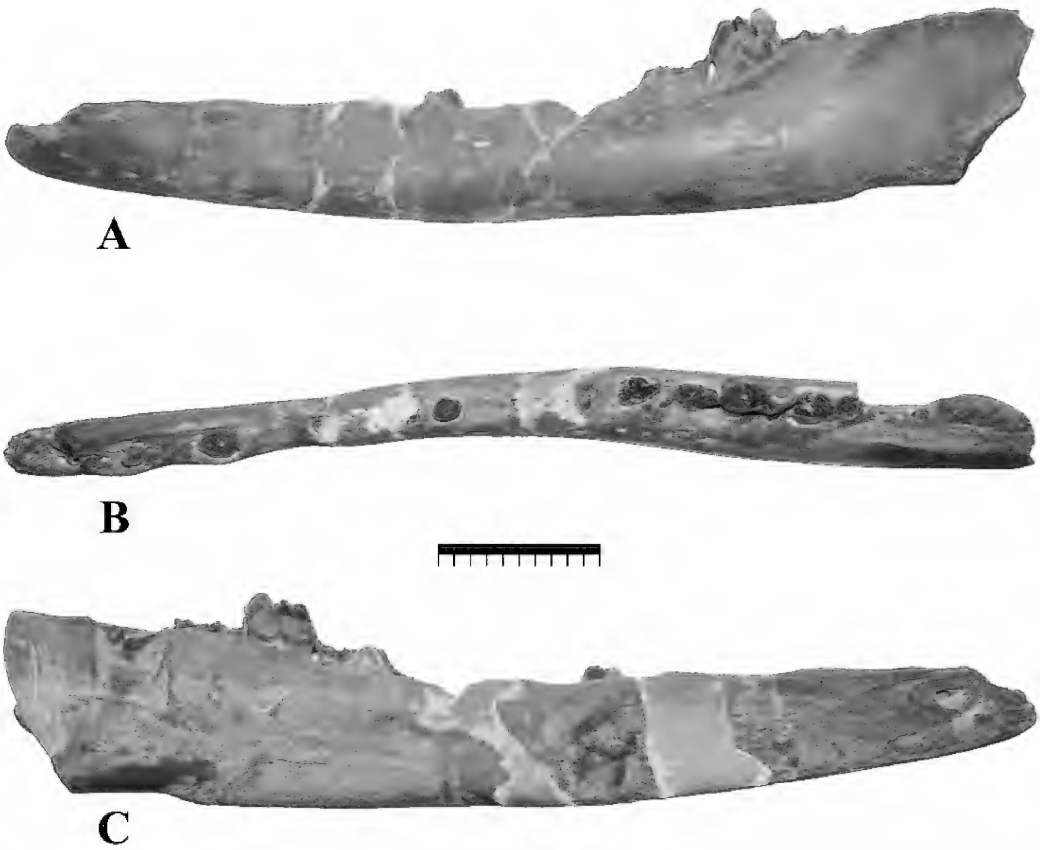

Figure 5 *Pappocetus lugardi* Andrews, 1920, referred specimen, BM(NH) M-11086, incomplete left dentary: **A,** labial view; **B,** occlusal view; **C,** lingual view. Scale bar = 10 cm.

the talonid cusp remains of the m1 crown. The m2 is complete except for a labial portion of its trigonid cusp. The entire m3 is present and is virtually unworn, except that the ventrolabial surface of the trigonid cusp and the anterior root have been sheared away.

Dorsoventrally, both dentaries gradually taper anteriorly, with the greatest preserved depth being at the midpoint of the angular process. Because both coronoid processes are broken, no maximum depth of the dentary can be determined at this location. The dentaries taper rather gradually to their anteriormost preserved portions. The external (lateral) surface of the posterior part of the dentary of *Crenatocetus rayi* is convex; it bows noticeably labially. In contrast, the same area on the dentary of *Pappocetus lugardi* is nearly flat.

The angular process curves ventrally relative to the ventral edge of the horizontal ramus of the dentary as far as it is preserved, and it is inflected medially, thus forming a very obvious ventral extension of the border of the dentary. In contrast, the dentary of *Pappocetus lugardi* at this point ascends, and this part of the dentary of *Georgiacetus vogtlensis* is smooth. The anteromedial portion of the angular process, preserved on both dentaries of *Crenatocetus rayi*, shows a prominent ridge, about 1 to 2 mm in height, which is broad posteriorly and sharply narrowed anteriorly. At the location where the ridge narrows to become about as wide as it is deep, it curves sharply dorsally, and terminates at approximately the level of the ventral margin of the mandibular foramen. A second, relatively stout ridge, more or less defines the dorsal border of the medial side of the angular process. This ridge begins about 3 cm posterior to the level of the anterior margin of the mandibular foramen and continues to the broken posterior edge of the angular process. It slopes more steeply on its dorsal side.

The dentary of *Georgiacetus vogtlensis* has no such modifications of its ventral border, which instead exhibits only a smooth and slight dorsal curvature proceeding posteriorly, and in this regard, it is the same as in more primitive archaeocetes, in the more derived and geochronologically later basilosaurid archaeocetes, and in the mysticetes and odontocetes. The dentary of

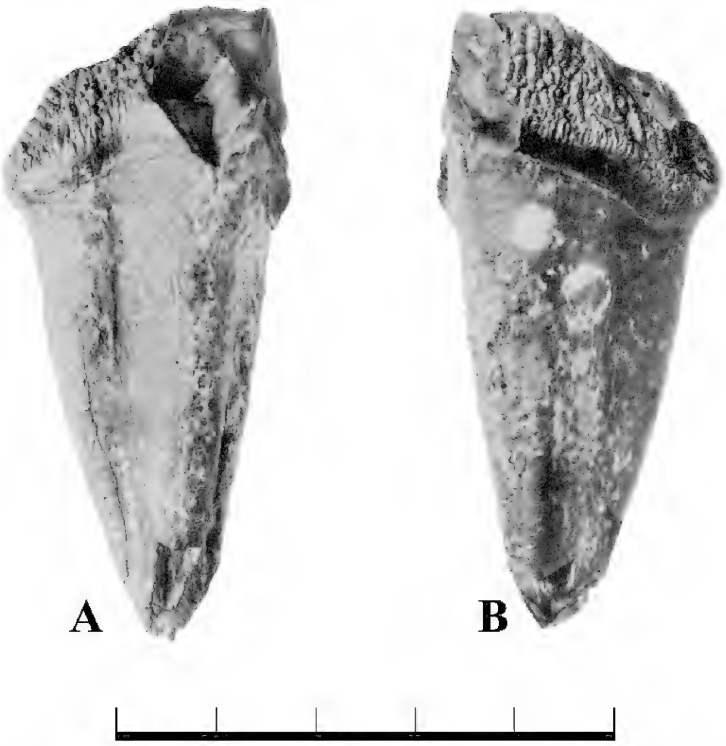

Figure 6 *Pontobasileus tuberculatus* Leidy, 1873, holotype, ANSP 11216, part of an originally two-rooted tooth, probably the anterior part of the trigonid of a right p4 with its anterior root: **A,** lingual view; **B,** labial view; modified from Kellogg (1936:pl. 36, figs. 4 and 5). Scale bar = 5 cm.

Pappocetus lugardi, on the other hand, has a different derived character, in which there is, in the posterior part, a notable dorsally ascending "steplike notch," which is the opposite of the ventrally extending crest in *Crenatocetus rayi*. These three character states serve to readily separate these three pappocetine species: *G. vogtlensis* having the primitive character state and *P. lugardi* and *C. rayi* each having alternate derived character states.

The mandibular foramen of *Crenatocetus rayi* is proportionally very large (Figs. 1C and 3C), and its aperture is approximately oval in shape. At the anteroventral margin of the medial lamina of the foramen, an indentation leads into a very shallow groove that is approximately 1 cm wide and extends anteriorly for approximately 2 cm. A shallow depression is immediately dorsal to and anterior to the mandibular foramen on the medial surface of the dentary. The area occupied by the mandibular foramen on the medial side of the dentary is greater in *C. rayi* than it is in *Georgiacetus vogtlensis*, the latter being more primitive in this regard. Both species have a small posterior projection of bone on the anterior border of the foramen, and this is located more ventrally in *C. rayi* than it is in *G. vogtlensis*.

In *Pappocetus lugardi*, the mandibular foramen is much smaller, and it is located much farther posteriorly on the dentary (see Fig. 7). The anterior margin of the mandibular foramen in *Crenatocetus rayi* is located far posterior to the last molar, being 64 mm posterior to the level of the posterior edge of m3. In *Georgiacetus vogtlensis* the anterior margin of the mandibular foramen is located more anteriorly (Fig. 7B). In contrast, in *P. lugardi*, the anterior margin of the mandibular foramen is located directly ventral to the posterior edge of m3 (Fig. 7C).

The coronoid crest of *Crenatocetus rayi* is thick and has a rounded anterior border. Enough of the base of the coronoid process is preserved to demonstrate that it is more steeply ascending than the coronoid process of *Georgiacetus vogtlensis* (Fig. 7). The presence of a more erect, and usually larger, coronoid process is a primitive state, present in terrestrial ungulates and in primitive protocetid cetaceans. Therefore, the less recumbent anterior border of the coronoid process in *C. rayi* is a more primitive character state than is that of *G. vogtlensis*. In *C. rayi* there is a wider space between the base of the coronoid process and the posterior edge of the m3 than in *G. vogtlensis*. In this character, *C. rayi* is the more

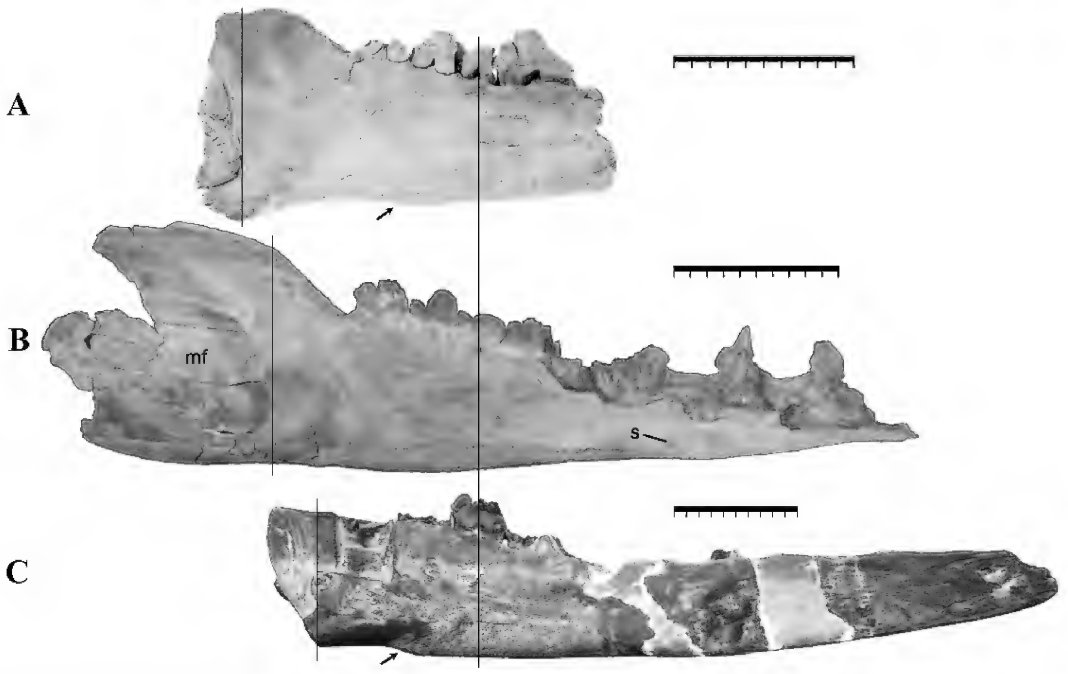

Figure 7 The left dentaries, in lingual views, of three species of Pappocetinae, to show their different proportions and different locations of the mandibular foramina. All three specimens are presented at the same dorsoventral height of the dentary at the middle of m1, between the two roots of this tooth, and are aligned at the middle of the m1. Each image has a vertical line drawn through the anterior border of the mandibular foramen. The steplike notch on the ventral border of the dentaries of *Pappocetus lugardi* and *Crenatocetus rayi* is indicated by an arrow. **A,** *Crenatocetus rayi*, new genus and new species, holotype, USNM 392014; **B,** *Georgiacetus vogtlensis*, Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998, holotype, GSM 350 (modified from Hulbert et al., 1998:fig. 7-2); **C,** *Pappocetus lugardi*, referred specimen, BM(NH) M-11086. **ABBREVIATIONS: mf** = mandibular foramen, s = posterior extent of mandibular symphysis. Scale bars = 10 cm.

derived taxon, and the wider space implies that the cranium would have had a more anteroposteriorly elongate temporal fossa than that of *G. vogtlensis*.

In the cheek tooth series from p4 to m3, the largest tooth is p4 and the smallest is m1. These teeth are two-rooted, and their crowns are positioned high above the dorsal margin of the dentary. The latter indicates substantial gum tissue between the tooth crowns and the bone in life.

All of the cheek teeth have distinct and complete labial and lingual cingula surrounding the bases of their crowns, and the cingula are ornamented with crenulated enamel and small cuspules. Compared with the same teeth of *Georgiacetus vogtlensis*, the cingula on the cheek teeth of *Crenatocetus rayi* are approximately twice the height dorsoventrally (or apicoproximally), and they are more rugose with tiny, but nonetheless clearly developed, cuspules. The remainder of each cheek tooth crown has enamel that is also crenulated, but not so much so as on the cingulid, and the crenulations on the apices of the crowns appear to be reduced by wear. Overall, the crenulation of the enamel of *C. rayi* is more prominent than on the teeth of *G. vogtlensis*.

In *Pappocetus lugardi*, the lingual cingula on p4 and m1–m3 arch apically between the roots. In contrast, in *Crenatocetus rayi*, the lingual cingula are nearly horizontal, arching only slightly. Each cheek tooth has two cusps: an anterior trigonid cusp and a posterior talonid cusp, the protoconid and hypoconid, respectively (see Gingerich and Russell, 1990). Typically, on the cheek teeth, the trigonid cusp is approximately twice the length and height of the talonid cusp. The offset between the cusps is only slightly anteroposterior, with the anterior portion of the protoconid and the posterior portion of the hypoconid being angled slightly lingually from the midline of the teeth. The anterior edge of the protoconid of each molar has an indentation or notch that receives the appressing hypoconid of the preceding tooth. This notch on each of these teeth is prominent, and it extends onto at least two thirds of the length of the root.

Because of this notch on the anterior side of each of the molar crowns, the anterior root of

Table 1 *Crenatocetus rayi* new genus and new species, measurements of the holotype, USNM 392014.

	Measurement (mm)
Left dentary	
Length as preserved at posterior p3 root fragment to midcoronoid process	253
Height as preserved at broken midcoronoid process	125
Height at base of p4	73
Width at broken midcoronoid process	45
Width at p4	38
Right dentary	
Length as preserved about level of p4 to close to articular condyle area	305
Height as preserved at broken midcoronoid process	134
Height at base of p4	74
Width at broken midcoronoid process	45
Width at p4	30
Height of mandibular foramen	84
Left p4	
Length of crown	53
Height of crown [worn]	31
Width of crown	15
Right m2	
Length of crown	31
Height of crown [broken]	26
Width of crown	12
Right m3	
Length of crown	33
Height of crown	29
Width of crown	15

each molar is expanded labiolingually. This transverse widening of the anterior part of the crown and the anterior root increases progressively posteriorly from the m1 to the m3. The anterior face of each molar crown is rugose, being bounded by cristids labially and lingually that project away from the rest of the protoconid, thereby making a cleft in the cingulid that extends apically, appearing as an inverted "V" on the crown in an anterior view. Both cristids bounding the cleft have fine, but not uniform serrations; small bulbous areas also appear on the cristids. The lingual cristid extends virtually to the apex of the trigonid cusp, but the labial cristid diminishes approaching the crown surface at a point approximately two thirds of the height of the crown.

A similar finely serrated cristid runs continuously in a posterior direction from the apex of the protoconid and down the midline of each tooth then continues over the apex of the hypoconid to merge with the posterior cingulid. This posterior cristid does not appear to have any of the slight bulbous projections such as are present on the anterior trigonid cristids. The juncture between the protoconid and hypoconid forms a deeply incised notch, in which the lowest point is above the middle of the posterior root, and the apex of the protoconid is above the separation between the anterior and posterior roots. Bone is invested in this area between the two roots of each tooth, and along with the depth of the conjunction of the roots in this area, this results in the uppermost parts of the roots, in addition to the crowns, being elevated above the level of the dentary, presumably indicating that, in life, a considerable amount of gum tissue existed between the dorsal margin of the dentary and the bases of the tooth crowns.

On the left p4 of *Crenatocetus rayi*, the apex of the protoconid is worn away, leaving an essentially flat wear surface that gently slopes posteriorly, but the apex of the much lower hypoconid is only slightly worn and slopes more steeply posteriorly. Three labial wear facets can be distinguished on this tooth: a small anterior facet that extends ventrally to the level of the cingulid, a middle facet that extends from the preserved apical protoconid ventrally toward the division between the roots but stops about 1 to 2 mm above the cingulid, and a small rounded posterior facet that is located half on the cingulid and half on the coronal surface below the apical wear facet. On all of these labial facets the crenulated surface is worn smooth, but with the possible exception of the anteriormost facet, the wear does not extend through the enamel. This tooth has only a single medial ridge, and a very rugose

expansion of the posterior part of the cingulid fits into the anterior notch of the m1. In dorsal view, the hypoconid and the posterior expansion of the rugose cingulid are angled more lingually on the p4 than on the molars. This projection is the only portion of the right p4 crown that is still present. On the left p4, a large sloping face of the protoconid extends out with the elongated root.

Although no notch is present on the anterior crown of the p4, there is a notchlike groove on the portion of the root exposed by breakage of the dentary, and a small portion of the posterior root of p3 is present in that groove. Because this groove is positioned more on the anterolabial portion of the root, it is likely, both phylogenetically and developmentally, that the original medial cristid was shifted lingually as the talonid of the preceding tooth became impressed first into the root and then into the crown of the tooth. The distinct cingulid is approximately 2 mm deep around the entire tooth. Delimiting the base of the crown, this cingulid is lowest at the anterior end of the tooth and rises at the area of the juncture of the two roots. It descends again toward the notch between the two cusps and finally rises at the posterior projection.

The p4 of *Crenatocetus rayi* has a definite and prominent bulge at its posterolingual corner, encompassing the cingulid in this area. Apical to the cingulid, part of the lingual side of the tooth is also convex and has several tubercles in the enamel. We interpret this as an autapomorphy of *C. rayi*. The posterolingual side of the p4 in *Pappocetus lugardi* is, in contrast, smoothly curved.

The proportions of the p4 of *Crenatocetus rayi* are significantly different from those of *Georgiacetus vogtlensis*. The measurements across the base of the crown of the p4 of *C. rayi* are 15 mm labiolingually by 53 mm anteroposteriorly; the width of the tooth being 28% of its length. The measurements across the base of the crown of the p4 of *G. vogtlensis* are 17 mm by 50 mm, the width being 34% of the length. Thus the p4 of *G. vogtlensis* is both proportionally and absolutely wider than in *C. rayi*. The larger but relatively narrower p4 of *C. rayi* is 2.08 times longer anteroposteriorly than the adjacent m1 (25.5 mm anteroposteriorly), whereas the smaller p4 of *G. vogtlensis* is 1.67 times longer anteroposteriorly than the m1 (30 mm anteroposteriorly).

Neither m1 is well preserved on the holotype of *Crenatocetus rayi*, with only the posterolingual portion of the right m1 present and most of the protoconid of the left m1 missing. A complete cingulid might have been present, as on the p4 and the other molars, and it is only slightly less deep than that on the p4. On the lingual surface of the left m1, the cingulid rises only slightly at the juncture between the roots, but it rises more steeply toward the posterior end of the tooth. Although broken, it is apparent that the anterior portion of the tooth slightly overhangs the posterior projection of the p4, which fits into the anterior notch of the left m1. The hypoconid is worn apically, but slopes ventrally anteriorly, in contrast to that of the p4. This cusp fits tightly into the anterior notch on the succeeding m2. A labial wear facet is present on the anterior half of the hypoconid. As noted in the preceding text, the anteroposterior crown length in *C. rayi* is 25.5 mm, versus 30 mm in *Georgiacetus vogtlensis*; thus, the m1 length of *C. rayi* is proportionally smaller.

Both the right and left m2 of *Crenatocetus rayi* have their labial surfaces broken away, but the right m2 retains most of the labial surface of the hypoconid, albeit worn. As opposed to the p4 and m1, the cingulid on the m2 does not rise in an arch at the juncture between the two roots, at least not on the preserved lingual portion of this tooth. It is instead horizontal. At the juncture between the two cusps, however, the cingulid rises posteriorly more sharply than it does on either the p4 or the m1. Both the right and left m2 show a prominent anterolingual trigonid cristid with irregular bulbous serrations. The apices of both of the cusps on the right m2 are worn, and they slope proximally toward the middle of the tooth. The preserved labial portion of the right m2 hypoconid has a wear fact on its anterior half.

Even though the m3 of *Crenatocetus rayi* is fully erupted, it is less worn than the other teeth. Only the roots of the left m3 are preserved, but the crown of the right m3 is nearly complete, having only slight abrasion and breakage on the labial portion of the anterior root and on the crown area directly above it. The cingulid is somewhat thicker dorsoventrally on the m3 than it is on either the m1 or the m2, being more than 5 mm high in the posteriormost portion. As with the m2, the cingulid on the m3 does not rise at the juncture between the roots on the lingual portion of the tooth, but it apparently rises slightly on the labial surface. At the juncture between the cusps, however, it rises abruptly and deepens. As with the m2, the anterolingual trigonid cristid is prominent, and it has irregular bulbous serrations. The anterolabial trigonid cristid is less well preserved because of abrasion, but it does show two small, but prominent, bulbous serrations that are worn. Although the protoconid has a slight, essentially flat apical wear facet, the hypoconid shows no apical wear. Because of the abrasion on the labial surface of the tooth, no wear facets are discernible.

Georgiacetus Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998

"middle Eocene archaeocete whales" (part). Petkewich and Lancaster, 1984:21.

"a middle Eocene (Lutetian) protocetid whale from Georgia." Hulbert and Petkewich, 1991:36A.

"a middle Eocene protocetid whale." Hulbert, 1993:42A.
"new genus." Hulbert, 1994:30A.
"a late middle Eocene protocetid cetacean." Hulbert, 1996:186.
Georgiacetus Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998:912. Hulbert, 1998; Geisler and Sanders, 2003.
Georaiacetus (lapsus). Uhen, 1999:table 1.

EMENDED DIAGNOSIS OF GENUS. The diagnosis of the genus shall remain identical to that of the type species until further species are described in the genus.

TYPE AND ONLY INCLUDED SPECIES. *Georgiacetus vogtlensis* Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998; type by monotypy.

AGE AND DISTRIBUTION. Middle Eocene, correlative with the late part of the Lutetian and/or the early part of the Bartonian stages, 40 to 41 Ma, Atlantic Coastal Plain, United States (Hulbert et al., 1998).

Georgiacetus vogtlensis Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998

Figure 7B

"middle Eocene archaeocete whales" (part). Petkewich and Lancaster, 1984:21.
"a middle Eocene (Lutetian) protocetid whale from Georgia." Hulbert and Petkewich, 1991:36A.
"a middle Eocene protocetid whale." Hulbert, 1993:42A.
"new genus." Hulbert, 1994:30A.
"a late middle Eocene protocetid cetacean." Hulbert, 1996:186.
Georgiacetus vogtlensis Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998:912, figs. 4–9, 11.
Georgiacetus vogtlensis Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998. Hulbert, 1998; Uhen, 1999; Geisler and Sanders, 2003.

EMENDED DIAGNOSIS OF SPECIES. A species of medium-sized pappocetine protocetids, having smaller adult body size than *Pappocetus lugardi* and apparently than *Pontobasileus tuberculatus* and similar in adult body size to *Crenatocetus rayi*; having cranium with condylobasal length of approximately 800 mm, with external naris located approximately midlength on rostrum with its posterior margin dorsal to P1, M3 present, greatly enlarged sagittal and nuchal crests, and large postglenoid process of squamosal; having dentary with greatly enlarged mandibular foramen, low coronoid process, and medially inflected angle of dentary; and having pelvis with functional acetabulum; differing from *C. rayi* by having dentary with narrower space between posterior edge of m3 and base of coronoid crest, less steeply ascending coronoid crest, relatively smaller mandibular foramen, smooth ventral margin of dentary posteriorly rather than prominent ventrally flaring crest ventral to the mandibular foramen, premolar and molar crowns wider labiolingually, with lesser development of crenulations on enamel, less prominent and less cuspate lingual and labial cingula that are proportionally approximately one-half the height dorsoventrally, and p4 relatively and absolutely smaller but proportionally wider labiolingually, and by lacking sulcus extending anteroventrally from anterior margin of mandibular foramen; differing from *P. lugardi* by having smaller adult body size, and by having smooth ventral margin of dentary posteriorly rather than pronounced steplike notch in ventral margin of dentary ventral to the position of m3, by having proportionally larger mandibular foramen whose anterior margin is much farther posterior, and having proportionally wider p4 in anteroposterior dimension; and differing from *P. tuberculatus* by apparently having smaller adult body size, by having p4 crown proportionally more compressed labiolingually, and by having cheek tooth crowns with less rugosely crenulated enamel and less cuspate labial and lingual cingula.

HOLOTYPE. GSM 350, partial skeleton, collected by Richard M. Petkewich, Gale A. Bishop, and a collecting crew from Georgia Southern University in 1983.

TYPE LOCALITY. Plant Vogtle of the Georgia Power Company, along the Savannah River, approximately 40 km southeast of Augusta, Burke County, Georgia, USA.

FORMATION AND AGE. The holotype is from the informally named Blue Bluff Unit, formerly a part of what was called the McBean Formation, middle Eocene, correlated with the late part of the Lutetian Stage and/or the early part of the Bartonian Stage (Hulbert et al., 1998).

COMMENTS. The geologic age and occurrence of the holotype as stated above are based on data from Hulbert et al. (1998). *Georgiacetus vogtlensis* is demonstrably the geochronologically earliest known species in the subfamily Pappocetinae. This is consistent with its possession of a suite of relatively primitive characters in comparison with the other species in the subfamily.

Georgiacetus vogtlensis is related to *Crenatocetus rayi*, but it differs from that species in some characters that are more primitive and in others that are more derived. The dentary of *G. vogtlensis* does not have a ventrally directed flange on its ventral margin, this flange being one of the apomorphies that defines *C. rayi*. The premolars and molars of *G. vogtlensis* are less embellished by extensively crenulated enamel and cuspate lingual and labial cingula than in *C. rayi*. The relatively smaller mandibular foramen (a primitive character state) of *G. vogtlensis* has an

anterior margin that extends farther anteriorly (a derived character state). It has a more recumbent anterior border of its coronoid process, and it apparently has a lower coronoid process compared with *C. rayi*, both of which are for *G. vogtlensis* the more derived character state.

Georgiacetus, aff. *G. vogtlensis* Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998

Protocetid cetacean. Albright, 1996.
Georgiacetus cf. *vogtlensis*. Uhen, 1999: table 1.

REFERRED SPECIMENS. ChM PV 5037, possible incisor; ChM PV 5038, possible right p2; ChM PV 5039, possible right m1; all collected by Mr. S. Peek of Summerville, South Carolina.

LOCALITY. Martin Marietta Berkeley limestone quarry, 2.4 km (1.5 miles) south of the intersection of South Carolina Highway 6 and County Road 59, Berkeley County, South Carolina, USA.

FORMATION AND AGE. These specimens are from the upper part of the Santee Limestone below the Cross Member (= Cross Formation), of middle Eocene age and correlated with the late part of the Lutetian and/or the early part of the Bartonian stages (Albright, 1996; Hulbert et al., 1998:fig. 2).

COMMENTS. Uhen (1999:table 1) reidentified these specimens as *Georgiacetus* cf. *G. vogtlensis*. We are more cautious, thus identifying them as *Georgiacetus* aff. *G. vogtlensis*. The geologic occurrence of these specimens is approximately temporally correlative with the occurrence of the holotype of *G. vogtlensis* (Albright, 1996; Hulbert et al., 1998:fig. 2), but they are from different rock units in different areas, whose ages might differ by as much as 3 million years.

The merged roots of the possible p2 (ChM PV 5038, Albright, 1996:fig. 3-3) are an odd character, possibly even a pathology or a genetic defect because they differ from the typically double-rooted second upper and lower premolars of archaeocetes. They are also a contrast with the distinctly separate roots of the supposed P1 of *Georgiacetus vogtlensis* (Hulbert et al., 1998:fig. 8-11). The p2 of *G. vogtlensis* would be expected to have had two separate roots, not two merged roots.

The right lower molar in this sample, ChM PV 5039, is more likely an m2, rather than an m1, as was determined by Albright (1996). This tooth is a near mirror image of the left m2 of the holotype of *Georgiacetus vogtlensis* (Hulbert et al., 1998:fig. 9-2). Both teeth have a deep notch between the talonid and trigonid; a lobate (rather than pointed) trigonid crown, which has a rounded apex, and a crenulate cristid ascending its anterior surface; and the characteristic noncuspate cingula and only slightly crenulate enamel that characterize the genus *Georgiacetus*.

Pappocetus Andrews, 1920

Pappocetus Andrews, 1920:309. Kellogg, 1936: 243; Barnes and Mitchell, 1978:585; Hulbert, 1998; Hulbert et al., 1998; Geisler and Sanders, 2003.

EMENDED DIAGNOSIS OF GENUS. The diagnosis of the genus shall remain identical to that of the type species until further species are described in the genus.

TYPE AND ONLY INCLUDED SPECIES. *Pappocetus lugardi* Andrews, 1920; type by monotypy.

AGE AND DISTRIBUTION. Middle Eocene, correlative with the late Lutetian Stage, Nigeria.

Pappocetus lugardi Andrews, 1920
Figures 4, 5, 7C

Pappocetus lugardi Andrews, 1920:309, text-fig. 1, pl. 1. Kellogg, 1928:38–39, 1936:243; Dechaseaux, 1961:845; Van Valen, 1966:90, 1968:37; Halstead and Middleton, 1974:81, figs. 4 and 5, 1976; Barnes and Mitchell, 1978:585–587, fig. 29-1; Hulbert, 1998; Hulbert et al., 1998; Geisler and Sanders, 2003.

DIAGNOSIS OF SPECIES. A species of large-sized pappocetine protocetids, larger as adults than *Georgiacetus vogtlensis* and *Crenatocetus rayi*, apparently similar in size to *Pontobasileus tuberculatus*; differing from *G. vogtlensis* and *C. rayi* by being approximately 1.5 times larger in adult body size and having a proportionally narrower p4 in anteroposterior dimension; differing further from *G. vogtlensis* by having a prominent steplike notch in ventral margin of dentary ventral to the position of m3, rather than a smooth ventral margin of dentary posteriorly; differing further from *C. rayi* by having a dentary with a pronounced steplike notch in the ventral margin of the dentary ventral to position of m3, rather than prominent ventrally flaring crest ventral to mandibular foramen; and differing from *P. tuberculatus* by having p4 crown more compressed labiolingually and cheek tooth crowns with less rugosely crenulated enamel and less prominently cuspate lingual and labial cingula.

HOLOTYPE. BM(NH) M-11414, incomplete mandible, consisting of parts of both the right and left dentaries, with two deciduous right premolars and four deciduous left premolars and a molar, collected by Sir Frederick Lugard.

REFERRED SPECIMENS. BM(NH) M-11086, incomplete left dentary with m1 and m3 partly erupted; BM(NH) M-11087, crown of probable incisor; BM(NH) M-11089, axis vertebra.

TYPE LOCALITY. From a railroad cut on the Port Harcourt Railroad, at Ameki, Ombialla District, southern Nigeria (Andrews, 1920; Kellogg, 1936:243).

FORMATION AND AGE. The holotype, paratype, and referred specimens are all from pyrite-rich clay of the Ameki Formation (see Reyment, 1965), and are middle Eocene in age, correlative with the late part of the Lutetian Stage (Kellogg, 1936:243; Van Valen, 1968:37; Halstead and Middleton, 1974, 1976; Hulbert et al., 1998:table 3).

COMMENTS. This is a relatively large protocetid, and it is the largest known pappocetine. When it was named by Andrews (1920), the only possible known relative was the smaller and geochronologically older (early Lutetian age) *Protocetus atavus* Fraas, 1904, from Egypt. Some earlier authors raised the issue that the two species defied comparison because *Protocetus atavus* was known only by a cranium, and *Pappocetus lugardi* was known only by a mandible. Kellogg (1936:279–280) regarded them as being distinct at the generic level. Van Valen (1966:90), however, questioned the validity of *Pappocetus lugardi*. Halstead and Middleton (1976:132) and Barnes and Mitchell (1978:585, 587) concluded that the two taxa are distinct, and our comparisons here support separation at the subfamilial level based on the highly derived dental characters of *Pappocetus lugardi*. With the discovery of additional protocetid archaeocetes, the distinction between *Pappocetus lugardi* and *Protocetus atavus* has been accepted by virtually all recent authors.

There might be some confusion about the shape of the dentary of *Pappocetus lugardi*. Re-preparation by the late Robert L. Clark, Jr., confirmed that the holotypic mandible was broken from geologic compression in two places, and the parts are displaced (Fig. 4; and see Halstead and Middleton, 1976:132). The undistorted referred left dentary (Fig. 5) confirms that, as would be expected for a cetacean, the dentary is elongate, has a nearly straight ventral margin, is compressed labiolingually, and tapers anteriorly. Also typical of cetaceans, the incisors and cheek teeth are aligned anteroposteriorly in a row, the mandibular symphysis is elongate, and the mandibular foramen is enlarged.

The holotypic left dentary of *Pappocetus lugardi*, BM(NH) M-11414, had retained, until our study, a remnant of sediment still adhering to the m1 (see Barnes and Mitchell, 1978:fig. 29.1a–c). We have removed this sediment (keeping it reposited in the BM(NH) with the specimen), thus allowing a more clear illustration of the posterior dentition of this specimen (Fig. 4).

The holotype is from a smaller individual than the referred dentary, and being less mature, its teeth are not as fully erupted. We agree with previous authors that the specimens do represent the same species.

The undeformed referred dentary has its anterior end and its symphyseal surface intact. Our preparation revealed that the break in the area of the p3 was correctly repaired and it has a good connection. The bone surface on the horizontal ramus is striated in a manner typical of later Odontoceti and Mysticeti. Other areas of the dentary have a porous surface, further indication of the young ontogenetic age of the animal. Twelve nutrient foramina are aligned along the labial surface of the horizontal ramus, and there was possibly a 13th foramen in a damaged area ventral to the p1. Most of the foramina open anteriorly, but the three posterior ones open posteriorly.

The surface of the mandibular symphysis extends posteriorly as far as the anterior margin of the anterior alveolus of p3. The dentary is concave along its ventromedial surface. The bone surface ventral to the mandibular foramen is dense and smooth, to the point of being glossy. In this respect, this part of the dentary resembles the "pan bone" of the later odontocetes, that part of the mandible that has been implicated in the reception of sound. The much-discussed steplike notch on the ventral margin of the dentary is located ventral to the position of the interalveolar septum that is between the m2 and the m3.

Some of the teeth have been misidentified. On the illustration of the holotype by Halstead and Middleton (1976:fig. 5a), each of the labeled teeth is actually the subsequent tooth. Thus the anteriormost tooth is not the canine, but the p1, and the last tooth in the left dentary is the m2. Their illustration of the referred left dentary (Halstead and Midddleton, 1976:fig. 4) is correct from the i3 to the p3, but what were labeled as the "Pm_4" and the "M_1" are, in fact, the anterior and posterior roots, respectively, of a large, two-rooted p4. Thus, the tooth that they label as the "M_2" is actually the m1. Repreparation of the specimen by Mr. Clark confirmed the existence of an unerupted m3 posterior to the partial tooth that Halstead and Middleton (1976:fig. 4) labeled "M_3." In our Figure 7C, the line passes through the m1 on the referred specimen.

On the referred dentary, BM(NH) M-11086, the i1 and i3 are small, and the i2 and canine are nearly twice their diameter. The deciduous i2 and i3 are *in situ*, and the apices of their roots are closed. The permanent i2 is visible in the alveolus, beneath the di2, through a hole that has been broken in the symphyseal surface. The permanent i3 is protruding posterior to the crown of the deciduous i3. All of the incisors and the canine are procumbent, and they are oriented anterolabially. The crowns of the premolars and the molars are all oriented vertically. The anterior teeth are all separated by diastemata, the largest of which is between the canine and p1. The diastema between the p1 and the p2 is, by comparison, relatively short. A short diastema is between p3 and p4, and the crowns of these two teeth do not touch. A small pit is on the lingual side of the pyramid of bone between the two roots of both the p2 and the p4. This area on the p3 is not preserved.

The p4 has an anomalous third root on its lingual side opposite the small pit. The presence of this third root is certainly an anomaly because even in terrestrial mammals, when the p4 is trenchant, it only has two roots. On the labial side of the dentary between the p4 and the m1 is an embrasure pit, which in life accommodated the crown of the opposing P4. The p4 and m1–m3 are all closely packed, and the crown of each of these teeth contacts its neighbor. The m1 is the only cheek tooth crown that is complete and it is fully erupted. It is very similar to the m1 of *Crenatocetus rayi* in the degree of the crenulations of the enamel, the size and development of the cingulid, the deep notch between the trigonid and the talonid, and the presence of the notch in the anterior side of the trigonid that accepts the posterior end of the p4.

The m2 and m3 are not fully erupted; the edge of the cingulid of each tooth was only beginning to appear above the labial alveolar rim. The crown of the m3 is badly damaged: most of the enamel is missing, and only the inner dentine remains. Before our preparation, someone had cut a hole into the lingual side of the dentary to observe the unerupted m3. Unfortunately, in doing so, most of the enamel of the crown was removed.

The referred isolated tooth crown, BM(NH) M-11087, is essentially complete. It was identified by Halstead and Middleton (1976:133) as a "canine milk tooth." The crown of the tooth is recurved posteriorly, and it has extending for its length a crista on the anterolingual side and another on the posterolabial side. Its cross section at the base of the enamel is nearly square, except that the anterolabial side is rounded. This tooth is probably an incisor, but it is not possible to confirm this because no incisors are present on the holotype and referred specimens. Its lingual side is flattened, and this suggests that it could be either a right I1 that was crowded against the suture between the right and left premaxillae at the tip of the rostrum, or a left i1 that was close to the mandibular symphysis. If it were a canine, we believe that its lingual side would not be flattened.

Pontobasileus Leidy, 1873

Pontobasileus Leidy, 1873:337.

Pontobasileus Leidy, 1873. Kellogg, 1936:265 (as a possible squalodontid related to *Squalodon tiedemani*); Gillette, 1975:65; Thurmond and Jones, 1981 (as an odontocete).

DIAGNOSIS OF GENUS. The diagnosis of the genus shall remain identical to that of the type species until further species are described in the genus.

TYPE AND ONLY INCLUDED SPECIES. *Pontobasileus tuberculatus* Leidy, 1873; type by monotypy.

AGE AND DISTRIBUTION. Possibly middle Eocene, probably the North American Gulf Coastal Plain.

Pontobasileus tuberculatus Leidy, 1873

Figure 6

Pontobasileus tuberculatus Leidy, 1873:337, pl. 37, fig. 15.

Pontobasileus tuberculatus Leidy, 1873. Kellogg, 1936:264–265 (as a possible squalodontid), table 69, pl. 36, figs. 4 and 5; Gillette, 1975:65; Thurmond and Jones, 1981 (as an odontocete).

DIAGNOSIS OF SPECIES. A species of large-sized pappocetine protocetids, larger as adults than *Georgiacetus vogtlensis* and *Crenatocetus rayi*, apparently similar in size to *Pappocetus lugardi*; differing from *G. vogtlensis*, *C. rayi*, and *P. lugardi* by having p4 1.5 times as wide labiolingually, and cheek tooth crowns with more rugosely crenulated enamel and more prominently cuspate lingual and labial cingula; apparently differing further from *G. vogtlensis* and *C. rayi* by having larger adult body size.

HOLOTYPE. ANSP 11216, part of an originally two-rooted tooth, probably the anterior part of the trigonid of a right p4 with its anterior root; collector and date unknown.

TYPE LOCALITY. The original ANSP label with the specimen says "Ala?" This indicates that the locality originally was uncertain but may be in the state of Alabama, USA. Leidy (1873; cited by Kellogg, 1936:265) supposed "it to have been derived from some Eocene or Miocene formation of the Atlantic States" and also stated that the specimen was found with some *Basilosaurus* specimens from Alabama.

FORMATION AND AGE. The original ANSP label with the specimen says "Miocene!" Kellogg (1936:265) noted Leidy's (1873) observation that the specimen has the attachment places for two barnacles (see Fig. 6B), and this supports his suggestion that the specimen might have been obtained by dredging operations near Charleston, South Carolina. If it were obtained from anywhere near Charleston, that would place it within the Atlantic Coastal realm that yielded *Georgiacetus vogtlensis* and *Crenatocetus rayi*.

Because the locality of *Pontobasileus tuberculatus* is not certain, the age is certainly speculative. Gillette (1975:65) listed the age as questionably Eocene. On the basis of the identification that we offer below and the apparent stage of evolution of the specimen, we speculate that it is possibly middle Eocene in age.

COMMENTS. Leidy (1873:337) astutely recognized that this was a cetacean when he commented that it "... apparently belonged to an animal of the same order as the *Basilosaurus*," and he also correctly recognized that it was an

originally two-rooted tooth. Kellogg (1936:264–265) described the specimen very accurately and presented measurements (Kellogg, 1936:table 69) and illustrations of it (Kellogg, 1936:pl. 36, figs. 4 and 5). Kellogg (1936:265) concluded that the specimen most closely resembles a low-crowned posterior lower molar of a squalodontid odontocete, and concluded that it "... may have belonged to a species related to or possibly identical with *Squalodon tiedemani* ..." From examining his detailed measurements (Kellogg, 1936:table 69) of the holotype, it is also clear that Kellogg regarded the specimen as being the posterior part of a tooth. Thurmond and Jones (1981:197) also suggested that *Pontobasileus tuberculatus* was an odontocete. Thus it has been overlooked in recent studies about archaeocetes and, surprisingly, it does not appear in Simpson's (1945) classification of mammals.

None of the researchers who previously considered the identity of *Pontobasileus tuberculatus* had the benefit of seeing the specimens that are now available of pappocetine protocetids. It is interesting that Leidy's (1873) original assessment of its relationships was the most nearly correct. The mistaken impression that it was a low-crowned tooth resulted because what remains of this tooth is only the sloping anterior part of the trigonid of what was a very large right p4 of a pappocetine protocetid archaeocete. Furthermore, we conclude that this very fragmentary specimen, while not totally desirable for a type specimen by the standards of today, can be distinguished from all other closely related cetaceans and thus represents a valid taxon. Thus, our diagnosis above.

The holotype of *Pontobasileus tuberculatus* resembles the anterior part of the trigonid of the right p4 of the holotype of *Crenatocetus rayi* by having very crenulate enamel, a well-developed and cuspate lingual cingulid, a slightly less prominent and less cuspate labial cingulid, and an anteroposteriorly aligned cristid that slopes anteriorly. These features are present only in pappocetine protocetids. The morphology of the root helps demonstrate that it is from the right side. This root resembles the anterior root of the holotype of *C. rayi*, and it is long, tapers apically, has a shallow longitudinal sulcus on its lingual side and a deeper longitudinal sulcus on its posterior side, and has a small isthmus of root material that originally was connected to the now missing posterior root. The tooth is generally much more massive than the corresponding tooth of *C. rayi*, and it is approximately 50% wider. For example, the preserved part of the trigonid of *P. tuberculatus* measures 17.2 mm in transverse (labiolingual) width, compared with 13 mm for the same width of the trigonid of the p4 of C. *rayi*.

Regardless of its geologic and geographic sources, the holotype of *Pontobasileus tuberculatus* is different from the cheek teeth of all other described species of archaeocetes. The holotype of *P. tuberculatus* indicates that its cheek teeth were more massive, were 50% wider labiolingually, and had more rugosely crenulate enamel and more prominently cuspate labial and lingual cingula than the cheek teeth of *Pappocetus lugardi*, *Georgiacetus vogtlensis*, or *Crenatocetus rayi*. The greater labiolingual width of the holotype tooth suggests that its adult body size might have been proportionally larger than those of *G. vogtlensis* or *C. rayi*. *Pontobasileus tuberculatus* is apparently a large species of, dentally, a relatively derived pappocetine protocetid.

DISCUSSION

In the past, there have been questions (e.g., Van Valen, 1966, 1968) about the taxonomic distinction between *Protocetus atavus*, which was originally based only on a cranium from Egypt, and *Pappocetus lugardi*, which was based on two mandibles from Nigeria. Although these two species were based on noncomparable typic material, it is now clear that they are distinct (see Barnes and Mitchell, 1978; Kumar and Sahni, 1986:345–346). The apparent dorsal inflection of the dentary in the symphyseal region of the holotype of *P. lugardi*, most recently queried by Kumar and Sahni (1986), is revealed on further cleaning of the holotype by us to be the result of breakage and geologic distortion (see also Halstead and Middleton, 1976). *Protocetus atavus* is the smaller of the two species, and it is more primitive dentally because its teeth have smoother enamel and the crowns are more conical and not so compressed labiolingually. *Pappocetus lugardi*, in addition to being a larger animal, is more derived, having teeth that have serrated cristae, strongly crenulated enamel, labiolingually compressed crowns, and prominent lingual and labial cingula that bear many small cuspules.

We consider that of all known archaeocetes, *Crenatocetus rayi* is most closely related to *Georgiacetus vogtlensis*. These two, along with the more derived *Pappocetus lugardi*, share derived characters that separate them from the other Protocetidae, and this affiliation is best reflected by establishing the new subfamily Pappocetinae to include these taxa. *Pontobasileus tuberculatus* is a larger pappocetine, and its cheek teeth have a greater development of the enamel crenulations and of the cingula.

Pappocetus lugardi is represented by specimens that are directly comparable with the holotype of *Crenatocetus rayi*, so these two species are demonstrably distinct. The original material of *P. lugardi* consists of the holotypic mandible, which is the medial portion of the left dentary and

a smaller attached portion of the right dentary, and a more complete referred left dentary. Both specimens represent juvenile animals on the basis of the unerupted m3 of each . The holotype of *P. lugardi* is from an ontogenetically younger animal than the referred specimen, with the crown of its m2 just beginning to emerge from its alveolus. Despite their relatively immature states, both specimens of *P. lugardi* are one-fourth to one-third larger than the holotype of *C. rayi*, which represents an adult or nearly mature animal. Therefore, at maturity, *C. rayi* was a considerably smaller animal than *P. lugardi*.

Although none of the cheek teeth of *Pappocetus lugardi* retain a complete crown and are subadult, there are proportional differences between the teeth of *Crenatocetus rayi* and *P. lugardi*. In *C. rayi*, the crown of the p4 is twice the length of the crown of the m1, whereas in *P. lugardi*, the crown of the dp4 is only 1.5 times the length of the m1. We believe this proportional difference still held, although it was probably diminished, in the as yet unknown permanent adult dentition of *P. lugardi*.

Pappocetus lugardi and *Crenatocetus rayi* both possess relatively stoutly constructed dentaries that are especially deep dorsoventrally in the posterior part of the horizontal ramus. In both species the posterior cheek teeth from p4 to m3 form a closed series, with p4 being the largest tooth, m1 the smallest, and m2 and m3 larger than the m1. The anteroposterior appression of the posterior cheek teeth of these species is so extreme that the talonid of each tooth is wedged into a notch in the anterior portion of the succeeding tooth. This notch in the anterior surface of each lower molar is a character present in other Protocetidae, and it was also retained in the more derived Basilosauridae.

In *Crenatocetus rayi*, the posterior cheek teeth, although labiolingually compressed, are large and possess apically lobate cusps. This lobate feature is particularly notable on the talonids. The trigonids and talonids are each composed of a single cusp with a cristid that extends continuously over the midline of the tooth from the basal anterolingual portion of the tooth, where it merges with the anterior cingulid, to the posterior cingulid. The cusps have essentially horizontal wear facets at their apices (i.e., they do not wear obliquely to form shearing blades).

In *Crenatocetus rayi*, *Georgiacetus vogtlensis*, and *Pappocetus lugardi* there is a small indentation in the anteroventral margin of the mandibular foramen that forms a broad but very shallow trough. This is a derived character that unites the three taxa, but *C. rayi* has the widest trough with the most distinctly formed ridges bounding the trough. Andrews (1920) made note of a supposed steplike notch in the ventral border of the dentary of *P. lugardi*, located anterior to the level of the mandibular fossa at about the level of m2. This feature is distinct on the referred dentary of *P. lugardi*, but it is not apparent on the much fractured holotype of *P. lugardi*. We have further prepared this part of the holotype, and we suspect that the absence of the steplike notch might result from poor preservation or geologic distortion. In *C. rayi* there is a slight and gentle upward curvature on the ventral border at the position ventral to the m2 and m3 when viewed laterally that abruptly descends again at a point anterior to the mandibular fossa. This dorsal curvature might be the homologue of the steplike notch in the ventral margin of the referred dentary of *P. lugardi*, and it is apparently absent in *G. vogtlensis*. Thus the steplike notch on the dentary is slight but perceptible in *C. rayi*, indiscernible in *G. vogtlensis*, and very distinct in *P. lugardi*.

Crenatocetus rayi lacks some of the more derived features of *Pappocetus lugardi* by being smaller, having a relatively large p4, and by lacking a pronounced steplike notch in the ventral margin of the posterior part of its dentary. *Crenatocetus rayi* has a more primitive mandibular morphology than either *Georgiacetus vogtlensis* or *P. lugardi*. The teeth of *C. rayi* and *G. vogtlensis* have similar morphologies but different proportions. The distance between the anterior margin of the mandibular foramen and the posterior end of the cheek tooth row is different in each of the three pappocetine (see Fig. 7). This indicates that their crania differed in the relative positions of the ear regions, the temporal fossa, and the zygomatic arch, and, by inference, that they differed in their temporal musculatures.

Fortunately, the mandible is reasonably well known for all three species. That of *Georgiacetus vogtlensis* is the most generalized because the ventral margin of the dentary is relatively smoothly curved. This is the primitive character state that is present in more primitive protocetid archaeocetes, in more derived basilosaurid archaeocetes, as well as in mysticetes and odontocetes. In *Pappocetus lugardi*, the ventral border of the dentary has the steplike notch posteriorly, and this is a derived character state that is unique to this taxon. In *Crenatocetus rayi*, the ventral border of the dentary has a relatively sharp, ventrally flared border ventral to the mandibular foramen, and that is a different derived character state is unique to this taxon.

Typically, the teeth of cetaceans are not regarded as being exceptionally diagnostic. In later Tertiary odontocetes, often it is the tooth count rather than tooth morphology that distinguishes species. In contrast, the species of *Crenatocetus*, *Georgiacetus*, *Pappocetus*, and *Pontobasileus* have exceptionally distinctive teeth: emphasized cusps and crests, crenulations and other ornamentation of the enamel, prominent labial and lingual cingula, and enhanced

deep notches between the cusps. These are derived character states, and they serve to unite these four species in a clade, thus our inclusion of them all in one protocetid subfamily, the Pappocetinae.

The Pappocetinae could have evolved from protocetine-like cetaceans through increase in body size and elaboration of the dentition. The autapomorphies of the Pappocetinae preclude them from being ancestral to any taxon among the more derived basilosaurid archaeocetes, and the dorudontine Basilosauridae are generally considered to be the sister taxon of the Neoceti, the odontocetes and mysticetes (Barnes and Mitchell, 1978; Barnes, 1990; Fordyce and Barnes, 1994; Barnes and Sanders, 1996a, 1996b, 1996c; Goedert and Barnes, 1996; Uhen, 1996a; Geisler and Sanders, 2003).

On the basis of the ratios of oxygen isotopes in its tooth enamel, Thewissen et al. (1996c) concluded that the protocetine protocetid *Rodhocetus kasrani* Gingerich, Raza, Arif, Anwar, and Zhou, 1994, was a fully marine-adapted cetacean that could drink and metabolize seawater. Extrapolating from this conclusion, it is probably safe to assume that other members of the protocetid subfamily Protocetinae were also fully marine. This group stands in contrast to the quadrupedal and much more primitive members of the archaeocete families Pakicetidae and Ambulocetidae, which appear to have been amphibious, ambulatory, and limited in dispersion by their ability to drink only fresh water. Although members of the Pappocetinae, with the exception of *Georgiacetus vogtlensis*, are not now well known morphologically, they are demonstrably more derived than the Protocetinae in mandibular and dental features, and they were presumably more aquatically adapted cetaceans. They are also the only known group of exclusively non-Tethyan protocetids, with *Pappocetus lugardi* being from the South Atlantic realm on the west coast of Africa and *Crenatocetus rayi*, *G. vogtlensis*, and *Pontobasileus tuberculatus* being from the North Atlantic realm on the east coast of North America. All previous records of Pakicetidae, Ambulocetidae, and the indocetine and protocetine Protocetidae are from deposits in and around the borders of the Tethys Sea, which is the apparent place of origin of the archaeocete whales (Gingerich and Russell, 1981; Gingerich and Uhen, 1996b, 1998; Thewissen et al., 1996a). The Pappocetinae, therefore, appear to represent the first group of relatively highly derived, fully marine, possibly pelagic protocetids to have dispersed to areas beyond the shores of the Tethys Sea.

With *Crenatocetus rayi*, *Georgiacetus vogtlensis*, and *Pontobasileus tuberculatus* all being from the southeastern United States, the greatest known diversity of the subfamily Pappocetinae is now documented to be in the Western Hemisphere. This places the area of greatest diversity geographically distant from the apparent site of the origination of the family Protocetidae, which is in eastern Tethys, and distant from the site of discovery of the most derived member, *Pappocetus lugardi*, which is in the eastern South Atlantic. This bolsters our suggestion above that the Pappocetinae were relatively derived protocetids, possibly pelagic, and indicates that the common ancestors of *C. rayi* and *P. lugardi* were highly mobile cetaceans, relatively highly adapted to the aquatic environment, and relatively widely dispersed. If this is the case, then other fossil members of the Pappocetinae should be expected to be from outside of the Tethys realm.

CLASSIFICATION OF THE ARCHAEOCETI

Several new genera and species of archaeocetes have been proposed in recent years and there is no recently published classification of the archaeocetes to the species level. Therefore, in order to put the genera and species of the Pappocetinae into taxonomic perspective within the Archaeoceti, we offer the following classification of the suborder Archaeoceti derived from our discussion above. The classification of Pakicetidae and Ambulocetidae is modified from Thewissen et al. (1996b), that of some of the other Protocetidae is derived from classifications of Gingerich and Russell (1990) and Gingerich et al. (1995), that of the Remingtonocetidae is derived from Kumar and Sahni (1986), that of the Dorudontinae is derived from Uhen (1996a, 2004), and that of the Basilosaurinae follows Kellogg (1936) and Barnes and Mitchell (1978). The sequence of taxa in this classification reflects most of the relationships that are depicted in the phylogenetic trees that were proposed by Uhen (1999:fig. 7) and by Uhen and Gingerich (2001:fig. 12). The classification that was presented by Geisler and Sanders (2003:27) was selective and included only taxa in their phylogenetic analysis. Authors and dates in parentheses following family and subfamily groups indicate names that are used at different ranks than originally proposed.

Order Cetacea Brisson, 1762
- Suborder Archaeoceti Flower, 1883
  - Family Pakicetidae (Gingerich and Russell, 1990) Thewissen, Madar, and Hussain, 1996
    - *Ichthyolestes* Dehm and Oettingen-Speilberg, 1958
      - *Ichthyolestes pinfoldi* Dehm and Oettingen-Speilberg, 1958
    - *Pakicetus* Gingerich and Russell, 1981
      - *Pakicetus attocki* (West, 1980)
      - *Pakicetus inachus* Gingerich and Russell, 1981

Nalacetus Thewissen and Hussain, 1998
Nalacetus ratimitus Thewissen and Hussain, 1998
Himalayacetus Bajpai and Gingerich, 1998
Himalayacetus subathuensis Bajpai and Gingerich, 1998
Family Ambulocetidae Thewissen, Madar, and Hussain, 1996
Ambulocetus Thewissen, Hussain, and Arif, 1994
Ambulocetus natans Thewissen, Hussain, and Arif, 1994
Gandakasia Dehm and Oettingen-Speilberg, 1958
Gandakasia potens Dehm and Oettingen-Speilberg, 1958
Family Remingtonocetidae Kumar and Sahni, 1986
Dalanistes Gingerich, Arif, and Clyde, 1995
Dalanistes ahmedi Gingerich, Arif, and Clyde, 1995
Remingtonocetus Kumar and Sahni, 1986
Remingtonocetus harudiensis (Sahni and Mishra, 1975)
Remingtonocetus sloani (Sahni and Mishra, 1972)
Andrewsiphius Sahni and Mishra, 1975
Andrewsiphius kutchensis Sahni and Mishra, 1975
Andrewsiphius sloani (Sahni and Mishra, 1972)
Andrewsiphius minor Sahni and Mishra, 1975
Attockicetus Thewissen and Hussain, 2000
Attockicetus praecursor Thewissen and Hussain, 2000
Family Protocetidae Stromer, 1908
Subfamily Indocetinae Gingerich, Raza, Arif, Anwar, and Zhou, 1993
Artiocetus Gingerich, ul Haq, Zalmout, Khan, and Malkani, 2001
Artiocetus clavis Gingerich, ul Haq, Zalmout, Khan, and Malkani, 2001
Indocetus Sahni and Mishra, 1975
Indocetus ramani Sahni and Mishra, 1975
Rodhocetus Gingerich, Raza, Arif, Anwar, and Zhou, 1994
Rodhocetus kasrani Gingerich, Raza, Arif, Anwar, and Zhou, 1994
Rodhocetus balochistanensis Gingerich, ul Haq, Zalmout, Khan, and Malkani, 2001
Qaisracetus Gingerich, ul Haq, Khan, and Zalmout, 2001
Qaisracetus arifi Gingerich, ul Haq, Khan, and Zalmout, 2001
Subfamily Protocetinae (Stromer, 1908) Gingerich and Russell, 1990
Takracetus Gingerich, Arif, and Clyde, 1995
Takracetus simus Gingerich, Arif, and Clyde, 1995
Protocetus Fraas, 1904
Protocetus atavus Fraas, 1904
Carolinacetus Geisler, Sanders, and Luo, 2005
Carolinacetus gingerichi Geisler, Sanders, and Luo, 2005
Natchitochia Uhen, 1998
Natchitochia jonesi Uhen, 1998
Babiacetus Trivedy and Satsangi, 1984
Babiacetus mishrai Bajpai and Thewissen, 1998
Babiacetus indicus Trivedy and Satsangi, 1984
Eocetus Fraas, 1904
Eocetus schweinfurthi Fraas, 1904
Eocetus wardii Uhen, 1999
Gaviacetus Gingerich, Arif, and Clyde, 1995
Gaviacetus razai Gingerich, Arif, and Clyde, 1995
Gaviacetus sahnii Bajpai and Thewissen, 1998
Subfamily Pappocetinae new subfamily
Georgiacetus Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998
Georgiacetus vogtlensis Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998
***Crenatocetus* new genus**
***Crenatocetus rayi* new species**
Pappocetus Andrews, 1920
Pappocetus lugardi Andrews, 1920
Pontobasileus Leidy, 1873 **new suprageneric assignment**
Pontobasileus tuberculatus Leidy, 1873
Family Basilosauridae Cope, 1868
Subfamily Dorudontinae (Miller, 1923) Slijper, 1936
Dorudon Gibbes, 1845
Dorudon serratus Gibbes, 1845
Dorudon atrox (Andrews, 1906)
Zygorhiza True, 1908
Zygorhiza kochii (Reichenbach, 1847)
?*Zygorhiza wanklyni* (Seeley, 1876)
?*Zygorhiza juddi* (Seeley, 1881)
Saghacetus Gingerich, 1992
Saghacetus osiris (Dames, 1894)
Ancalecetus Gingerich and Uhen, 1996
Ancalecetus simonsi Gingerich and Uhen, 1996
Chrysocetus Uhen and Gingerich, 2001
Chrysocetus healyorum Uhen and Gingerich, 2001

Subfamily Basilosaurinae (Cope, 1868) Barnes and Mitchell, 1978.
Basilosaurus Harlan, 1834
Basilosaurus drazindai Gingerich, Arif, Bhatti, Raza, Anwar, and Sanders, 1997
Basilosaurus cetoides (Owen, 1839)
Basilosaurus isis (Andrews, 1904)
Basiloterus Gingerich, Arif, Bhatti, Raza, Anwar, and Sanders, 1997
Basiloterus hussaini Gingerich, Arif, Bhatti, Raza, Anwar, and Sanders, 1997
Cynthiacetus Uhen, 2005
Cynthiacetus maxwelli Uhen, 2005
Pontogeneus Leidy, 1852
Pontogeneus brachyspondylus (Müller, 1849)

CONCLUSIONS

1. A new genus and species of relatively derived fossil protocetid archaeocete whale, here named *Crenatocetus rayi*, is represented by two associated partial dentaries of the same individual, bearing teeth, apparently of late middle Eocene age, from the Atlantic Coastal Plain of the southeastern United States. Other Protocetidae have been reported from North America (*Pontobasileus tuberculatus*, *Georgiacetus vogtlensis*, *Natchitochia jonesi*, *Eocetus wardii*), and this is the fifth member of this family to be named from the western North Atlantic realm.
2. The exact source of the holotype and only known specimen of *Crenatocetus rayi* is not known, but anecdotal and geologic information suggests that it probably came from the Martin Marietta Company's New Bern Quarry at New Bern, Craven County, North Carolina. If this is correct, then the specimen was most likely derived from the Comfort member of the Castle Hayne Formation of late middle Eocene age (Lutetian or Claibornian correlative).
3. *Crenatocetus rayi* is a medium-sized archaeocete, having an estimated adult skull length of approximately 750 mm. It is characterized by a dorsoventrally deep dentary with a sharply deflected ventral border ventral to the mandibular foramen (an autapomorphy), a standard primitive eutherian dental formula, relatively large teeth with finely crenulated enamel, and labiolingually compressed cheek tooth crowns having cuspate lingual and labial cingula.
4. *Crenatocetus rayi* is related to the apparently geochronologically earlier middle Eocene *Georgiacetus vogtlensis* from Georgia, and the two differ in both primitive and derived characters. The two have similar dental morphology, but *C. rayi* has a larger p4, and *G. vogtlensis* has a smooth ventral border of the dentary, lacking the ventral expansion of the dentary that is present in *C. rayi*. The distance between the margin of the mandibular foramen and the posterior end of the cheek tooth row is different between these two species, and *C. rayi* apparently had a larger coronoid process, thus indicating that their crania must have been different in the area of the temporal fossa and the zygomatic arch, and, by inference, they would have had different temporal musculature.
5. *Crenatocetus rayi* is related to, but relatively more primitive than, *Pappocetus lugardi*, a middle Eocene protocetid known by at least three specimens from the Ameki Formation from the Ombialla District of Nigeria on the west coast of Africa. Compared with *P. lugardi*, *C. rayi* is smaller at maturity, has a proportionally larger p4, and does not have a steplike notch in the ventral margin of the posterior part of its dentary. In these characters, *C. rayi* is morphologically more primitive than *P. lugardi*. Because the general evolutionary trend among archaeocetes appears to have been for increasing body size through time, we also conclude that the smaller size of *C. rayi* is a primitive character state compared with the large size of *P. lugardi*.
6. The enigmatic cetacean *Pontobasileus tuberculatus* is referred to the subfamily Pappocetinae. The holotype is a partial two-rooted lower cheek tooth, probably the anterior part of the trigonid of a right p4, and the crown bears the distinctive crenulate enamel and prominent cuspate lingual and labial cingula that are characteristic of pappocetine protocetids. These features are more exaggerated than in the species of *Crenatocetus*, *Georgiacetus*, and *Pappocetus*. This and its proportionally wider p4 serve to distinguish it from the other three genera. The type locality of *P. tuberculatus* might have been in Alabama or on the Atlantic Coastal Plain. The stage of evolution of the specimen suggests that it is no older than middle Eocene in age.
7. The genera *Crenatocetus*, *Georgiacetus*, *Pappocetus*, and *Pontobasileus* are united with in the new subfamily Pappocetinae of the family Protocetidae. The Pappocetinae differ from other Protocetidae by having closely spaced fourth premolars and first through third molars with a deeply incised notch on the anterior of each molar to receive the talonid of the preceding tooth, prominently crenulate enamel on their teeth, and rugose and cuspate labial and lingual cingula on their cheek tooth crowns, all of which are derived characters. These derived characters also separate the Pappocetinae from the later basilosaurid archaeocetes and preclude their

being possible ancestors of them or of any of the later and more derived Cetacea. The Pappocetinae were a uniquely derived group of protocetid archaeocetes, and they have no known descendants.

8. The Pappocetinae are known only from deposits that are outside the ancient Tethys Seaway in the coastal eastern South Atlantic and coastal western North Atlantic. Their distribution suggests that this was a group of relatively highly derived Protocetidae that had developed a more pelagic mode of life than other primitive protocetids and that they had dispersed beyond the confines of the Tethys Sea where archaeocetes apparently originated.

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Miocene and Pliocene Albireonidae (Cetacea, Odontoceti), rare and unusual fossil dolphins from the eastern North Pacific Ocean

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ABSTRACT. Species of the cetacean family Albireonidae are extinct, medium-sized dolphins in the odontocete superfamily Delphinoidea. Their fossils are found in late Miocene and Pliocene marine rocks bordering the North Pacific Ocean, in California, USA; Baja California, Mexico; and Hokkaido, Japan. The best known species, *Albireo whistleri* Barnes, 1984a, was based on a nearly complete holotypic skeleton from the lower part (~6–8 Ma) of the latest Miocene age Lower Member of the Almejas Formation on Isla Cedros, Baja California, Mexico. Three additional albireonid specimens, some not clearly of this species, are from stratigraphically higher in the same formation. A more primitive albireonid, *Albireo savagei*, sp. nov., occurs in the late Pliocene (~2–3 Ma) Squire Member of the Pismo Formation in coastal central California. Species of *Albireo* have a combination of primitive and derived characters, some of which occur convergently in other odontocetes. The adult body of *A. whistleri* was approximately 2.5 m in length, stoutly built, deep in the thorax, with a relatively short neck and broad fore-flippers. The overall shape of the cranium, particularly the elevated and rounded occipital shield, is convergent with the Recent Dall's porpoise (*Phocoenoides dalli*, family Phocoenidae). The cranium has large-diameter bony nares that are circular in transverse cross section, large orbits, raised eminences on the premaxillae anterior to the narial openings, wide and thin posterior premaxillary terminations, flat and thin nasal bones, exposed frontal bones on the posterior wall of the narial passage, wide and flat exposures of the frontal bones on the cranial vertex, frontal bones comprising the dorsalmost part of the cranial vertex, mesorostral groove open dorsally only in the anterior one third of the rostrum, a line of foramina on the dorsal surface of rostrum along the suture between each maxilla and premaxilla, dorsoventrally thick lateral margin of the maxilla on the proximal part of the rostrum, dorsally curved rostral extremity, relatively large brain case, but it lacks the supraorbital lobe of the pterygoid air sinus system (a character of Phocoenidae), and an anterior sinus (a character of Delphininae). The premaxillae, nasals, and frontals around the narial openings are flattened in a manner not known in other cetaceans. The dentition is homodont and polydont, the tooth enamel is smooth, the tooth crowns conical, and there were approximately 25 teeth on each side of the palate and demonstrably 25 teeth in each dentary. By lacking extensive fossae for basicranial air sinuses, albireonids are more primitive than other delphinoid families; the extinct Kentriodontidae; and the extant Monodontidae, Phocoenidae, and Delphinidae. The cervical vertebrae are much compressed anteroposteriorly, but only the second and third cervical vertebrae are fused. The thoracic and lumbar vertebrae are increased in number and, in a manner similar to the extant bottlenose dolphin (*Tursiops truncatus*, family Delphinidae), are moderately compressed anteroposteriorly and have elongate transverse and neural processes. The basihyal and thyrohyal bones are very wide and flat. The first rib is very wide transversely and very thin anteroposteriorly. There are 16 thoracic vertebrae, of which the first nine have both capitular and tubercular articulations with the ribs, and the posterior seven have only tubercular attachments. The scapula is high proximodistally and narrow anteroposteriorly. The distal end of the humerus is very wide, and the distal ends of the radius and ulna are flat and expanded anteroposteriorly, much as in the unrelated, extant Ganges River dolphin (*Platanista gangetica*, family Platanistidae) and Amazon River dolphin (*Inia geoffrensis*, family Iniidae). Albireonid dolphins were probably pelagic in distribution. This odontocete clade existed for at least 6 or 7 million years and apparently has no living descendants.

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INTRODUCTION

The family Albireonidae is a group of extinct Odontoceti that is classified in the superfamily Delphinoidea, and the type genus of the family is *Albireo* Barnes, 1984a. Albireonids are medium-sized dolphins that lived in the North Pacific Ocean from at least late Miocene time to late Pliocene time, from approximately 9 to 2 or 3 million years ago. These cetaceans are rare in the fossil record, and the family Albireonidae has remained somewhat enigmatic since it was named by Barnes in 1984.

Albireo whistleri Barnes, 1984a, is the only previously named species in the family Albireonidae. The holotype of this species is, however, one of the best preserved and most nearly complete skeletons of any fossil cetacean from anywhere in the world (Barnes, 2002a). It was collected by David P. Whistler from the latest Miocene age (6–8 Ma) basal part of the Lower Member of the marine Almejas Formation on Isla Cedros, an island in the eastern North Pacific Ocean off the west coast of Baja California, Mexico (Fig. 1; see also Barnes, 1988a, 1988c, 1998, 2002c). The fossil marine vertebrate assemblage from these strata, known as the Isla de Cedros Local Fauna (Barnes, 1998), has become a standard of comparison for marine vertebrate fossils of this age in the North Pacific realm (Barnes, 1997a, 2002c:137).

David P. Whistler and George T. Jefferson, of the University of California at Riverside, were shown the fossiliferous outcrops on Isla Cedros by Frank H. Kilmer after he had discovered them and made a preliminary collection of marine vertebrate specimens in February 1964. The holotypic skeleton of *A. whistleri* is one of the most significant specimens that was collected on Isla Cedros during a preliminary expedition to the island in July 1964 by Whistler and Jefferson. This skeleton (Figs. 3–5) acquired the nickname in the field and in the laboratory as "Whistler's Porpoise."

In August of the following year (1965) a larger group of paleontologists, this time under the direction of Richard H. Tedford, and again including David P. Whistler, returned to the island and obtained a more extensive collection of marine vertebrate fossils. Among these fossils, only three isolated tympanic bullae are related to *A. whistleri*, and no additional fossils of this taxon appear to have been acquired during subsequent collecting trips to Isla Cedros in 1992, 1993, and 1995 (Barnes, 1993, 1998, 1999, 2002c; Barnes and González-Barba, 1993; Aranda-Manteca and Barnes, 1995; Barnes et al., 1997; Gascón-Romero et al., 1997; Flores-Trujillo et al., 1999, 2001).

The nearly complete anterior part of the holotypic skeleton of *A. whistleri* allowed the creation of a reconstruction of the animal's body shape when alive (Folkens et al., 1989), and illustrations of this remarkable fossil skeleton have several times been published (Barnes, 1992a:fig. 7, 2002c:figs. 8, 11g, 11h; Fordyce and Barnes, 1994:fig. 2b; Fordyce et al., 1995:fig. 3b; Berta and Sumich, 1999:fig. 4.30). However, the individual postcranial bones have not been previously described nor illustrated in detail.

Barnes (1988a, 1988c; Fordyce and Barnes, 1994:439) reported the discovery in the late Pliocene Pismo Formation near San Luis Obispo in central California of a second species of the Albireonidae, which was, until this writing, unnamed. This fossil includes the cervical and thoracic vertebrae and ribs of one individual. They document a geochronologically late occurrence of the genus *Albireo* and of the family Albireonidae, thereby expanding our knowledge of its geographic and chronologic distributions. Barnes and Furusawa (2001a, 2001b) have also reported a primitive albireonid of late Miocene age from Hokkaido, Japan, and that specimen is being described separately.

The purpose of this paper is to provide a detailed description of the excellently preserved and highly informative holotypic skeleton of *A. whistleri*; to make interpretations of the morphology, behavior, ecology, and function of this cetacean; to document additional specimens of *Albireo* from Isla Cedros, Mexico; and to describe the other species of *Albireo* from the Pliocene Pismo Formation in central California.

METHODS AND MATERIALS

ABBREVIATIONS

LACM	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
UCR	Locality records formerly maintained at the Department of Geological Sciences at the University of California, Riverside, California, and now maintained at the Museum of Paleontology, University of California, Berkeley California USA

Anatomical Abbreviations

Abbreviations used in Figures 11, 13, and 15.

Al	alisphenoid bone
ams	anteromedial sulcus on premaxilla
aon	antorbital notch
aopf	antorbital process of frontal
bc	basioccipital crest
Bo	basioccipital bone
ch	cranial hiatus (combined anterior lacerate foramen and posterior lacerate foramen)

eam	external acoustic meatus
ffr	frontal foramen
fh	hypoglossal foramen
fio	infraorbital foramen
fm	foramen magnum
fmxa	anterior maxillary foramen
fmxp	posterior maxillary foramen
fop	optic foramen
fpmx	premaxillary foramen
fppal	posterior palatine foramen
Fr	frontal bone
gf	glenoid fossa
Ju	jugal bone
jn	jugular notch
La	lacrimal bone
Me	mesethmoid bone
mrg	mesorostral groove
ms	bony fossa that contained the middle sinus, or the tympanosquamosal recess
Mx	maxillary bone
n	narial passage
Na	nasal bone
Oc	occipital bone
occ	occipital condyle
Pa	parietal bone
Pal	palatine bone
pls	posterolateral sulcus on the premaxilla
pms	posteromedial sulcus on the premaxilla
Pmx	premaxillary bone
pop	paroccipital process
popf	postorbital process of frontal
Pt(ll)	pterygoid bone, lateral lamina
Pt(ml)	pterygoid bone, medial lamina
pts	bony fossa that held the pterygoid sinus
sopf	supraorbital process of frontal
Sq	squamosal bone
sqf	squamosal fossa
Tb	tympanic bulla
Vo	vomer bone

Terminology for cranial anatomy follows Kellogg (1927), Fraser and Purves (1960), and Barnes (1978, 1985c). Cranial measurements were made following the methodology that was explained by Perrin (1975). Some anatomical comparisons have been made with specimens of certain Recent cetaceans. Authorship and nomenclature of family groups and of modern taxa follows Hershkovitz (1966) and Rice (1998).

The holotypic skeleton of *A. whistleri* was partly disarticulated, although definitely associated (Fig. 4), when it was found in the sediments on Isla Cedros. It was collected in field plaster jackets, and this method preserved the orientation of the bones. While the holotypic skeleton was being prepared in the laboratory of UCR, archival photographs were made showing the orientation of the bones in the sediment. Copies of the photographs are maintained in the UCMP files and with the specimen, and one of these photographs, included here as Figure 5, shows the bones of the thoracic area. Many of the bones have numbered paper labels glued to them, and these served to identify the bones in the photographs and, in some situations, to aid in determining their anatomical positions. I have identified the positions of vertebrae, ribs, sternal ribs, and phalanges partly with the aid of these photographs and also on the basis of comparisons with articulated skeletons of Recent Cetacea. I have written in ink directly on the bones their anatomical positions. It is possible that some of these bones are not precisely identified. Most of the vertebrae were in sequence when excavated, so their sequence has probably been determined correctly to within one or two positions. The sternal ribs decrease in size posteriorly, and these are identified for their approximate positions.

The cleaned bones of the skeleton were articulated in a sand box according to interpretations of their positions as explained above and then photographed to produce color transparencies. These transparencies were then projected onto paper, and the drawn skeletal reconstructions (Fig. 6) were created by tracing around the images and rearranging the positions of the bones.

The rendered line drawings (Figs. 10, 12, 14, 19, 22) are orthographic projections made by J. Patricia Lufkin. The cranial reconstructions (Figs. 11, 13, 15), prepared by the author, are based on these and are corrected to compensate for some geologic distortion; missing parts of the holotypic cranium were transposed between the two sides of specimen to create the most complete views of the cranium possible. The cranium is slightly crushed obliquely in the sagittal plane, the basioccipital crests and pterygoid sinuses are displaced to the left side, and the rostrum is bent to the left side relative to the braincase. Because of this distortion, neither antorbital notch is preserved correctly, and the reconstructions in Figures 11 and 15 are a compromise between the right and left sides. The left zygomatic process of the squamosal suffered preburial abrasion, and the photograph of the lateral side of the cranium in Figure 8b is made from a reversed negative of the right side of the cranium. The reconstructed outline of the zygomatic process in Figure 12 is based on the complete right side.

The only parts of the cranium that remain speculative are the ventral margins of the medial lamina of the pterygoids, the posterior tips of the pterygoid hamulae, and the anterior extremity of the rostrum.

Most of the teeth were not in place in the specimen. A few were in mandibular alveoli, but none remained in the rostrum. There are enough teeth to indicate the range in size and shape, and the bony dental alveoli indicate that the teeth were smaller at both the anterior and posterior ends of the tooth rows. Therefore, the only teeth that are truly speculative in the reconstructions are those in the missing anterior part of the rostrum.

While on Isla Cedros in 1964 and 1965, Richard H. Tedford and Frank H. Kilmer constructed stratigraphic columns of the Almejas Formation, recognized different lithologic units, and correlated these units between different outcrops within a relatively small geographic area. For this paper, I provide generalized stratigraphic columns (Figs. 1 and 2) from their field notes and have shown on them the stratigraphic occurrences of the holotype and other specimens of *Albireo*. A similar illustration was presented in an earlier paper (Barnes, 1984a), that included the stratigraphic positions of other cetacean taxa in the assemblage. Stratigraphic thicknesses are given in feet because that is how they were estimated by the original collectors. These stratigraphic thicknesses do not agree exactly with the maximum thicknesses of the members of the Lower Member of the Almejas Formation that were given by Kilmer (1979:19), but they must suffice pending a more detailed stratigraphic study of the outcrops.

SYSTEMATIC PALEONTOLOGY

Order Cetacea Brisson, 1762

Suborder Odontoceti (Flower, 1865) Flower, 1867

Superfamily Delphinoidea (Gray, 1821) Flower, 1865

INCLUDED FAMILIES. Albireonidae, Kentriodontidae, Odobenocetopsidae, Monodontidae, Delphinidae, and Phocoenidae (see Barnes, 1984b; Muizon, 1988; Fordyce and Barnes, 1994; Rice, 1998:table 5; Barnes, 2002b; Muizon and Domning, 2002).

Family Albireonidae Barnes, 1984a

Albireonidae, as a family of the Delphinoidea, Barnes, 1984a:29, 1984b, 1990:20, 2002a:208, 2002b:314–315, 2002c:163, 187; Fordyce and Barnes, 1994:439, table 1, figs. 1 and 3; Fordyce et al., 1995:table 1; Rice, 1998:table 5, 152; Barnes and Furusawa, 2001a, 2001b; Fordyce, 2002:463; Perrin et al., 2002:inside front cover.

Albeirodontidae (*sic*) Berta and Sumich, 1999: 75, 481.

TYPE AND ONLY INCLUDED GENUS. *Albireo* Barnes, 1984a.

DISTRIBUTION. Late Miocene, Hokkaido, Japan; latest Miocene, Isla Cedros, Baja California, Mexico; and late Pliocene, central California, USA.

DIAGNOSIS OF FAMILY. The family diagnosis shall remain identical to that of the genus *Albireo* until further genera are described in the family.

DISCUSSION. The name used in error by Berta and Sumich (1999:75, 481), Albeirodontidae, was intended to refer to this family. The family Albireonidae has been recognized as valid in the classifications that have been presented by Fordyce and Barnes (1994), Fordyce et al. (1995), Rice (1998:152), Barnes (2002b, 2002c), and Perrin et al. (2002). The discovery of an as yet undescribed late Miocene albireonid from Hokkaido, Japan (Barnes and Furusawa, 2001a, 2001b), and the description herein of a late Pliocene albireonid from California increase the taxonomic and morphologic diversity of the family and its geographic and chronologic ranges.

Genus *Albireo* Barnes, 1984a

Albireo Barnes, 1984a:31, 2002c:163, 187; Fordyce and Barnes, 1994:439; Rice, 1998:152; Fordyce, 2002:463.

TYPE SPECIES. *Albireo whistleri* Barnes, 1984a; type by original designation.

INCLUDED SPECIES. *Albireo whistleri* Barnes, 1984a, and *Albireo savagei*, sp. nov.

EMENDED DIAGNOSIS OF GENUS. A genus of Delphinoidea including medium-sized dolphin-like odontocete cetaceans having crania with premaxillary eminences present anterior to narial openings, posterior premaxillary termination on each side contacting the corresponding nasal bone, nasal bones very flat and wide, nasal bones separated from mesethmoid bone by a surface exposure of frontal bone on the posterior wall of narial passage, frontal bones rather than nasal bones comprising highest part of cranial vertex, frontal bones wide and flat on cranial vertex, braincase transversely widened, maxillary foramina enlarged, posterior premaxillary terminations large and transversely widened, rostral extremity curved dorsally, antorbital notch wide and open anteriorly, exposure of premaxilla on anterior part of palate extending posteriorly to contact the palatal exposure of vomer bone very wide and elongate, posterior part of palate relatively wide, diastem between posterior end of palatal alveolar row and antorbital notch, posterior margin of rostrum thickened dorsoventrally and flattened on the lateral surface, interalveolar septa lacking between teeth in palatal tooth row, lateral rostral margins of maxillary alveoli retracted dorsally, posterior maxillary foramen relatively anteriorly positioned at a location lateral to nares, maxillary surface elevated around dorsal apertures of anterior maxillary foramina, orbit relatively large, bony orbit lacking any bony fossa for supraorbital lobe of pterygoid air sinus system, squamosal lacking shelf medial to glenoid fossa delimiting lateral border of middle sinus (or tympanosquamosal recess), zygomatic process of jugal flattened mediolaterally and originating medial to antorbital notch; dentary with mandibular symphysis unfused, symphyseal region dorsally curved at anterior end, large mandibular symphysis that extends for approximately one fourth of the length of the dentary, mandibular

Table 1 The aggregate assemblage of fossil marine vertebrates from the Lower Member of the Almejas Formation, latest Miocene age, on Isla Cedros, Baja California, Mexico.

Hydrolagus sp. [chimera]
Heterodontus sp. [horn shark]
Scyliorhinidae, genus and species undetermined [cat shark]
Mustelus sp. [leopard shark]
Cetorhinus sp. [basking shark]
Isurus oxyrinchus [bonito shark]
cf. *Lamna* sp. [sand tiger shark]
Carcharodon cf. *C. carcharias* [extinct great white shark]
Carcharocles megalodon (Agassiz, 1837) [mega-tooth shark]
Carcharhinus sp. [reef shark]
Hexanchus sp. [six-gill shark]
Centrophorus sp. [gulper shark]
Squatina sp. [angel shark]
Rhinobatidae, genus and species undetermined [guitar fish]
Raja sp. [skate]
Myliobatis sp. [eagle bat ray]
Dasyatis sp. [sting ray]
Gymnura sp. [butterfly ray]
Mobula sp. [manta ray]
Clupeiformes, genus and species undetermined [herring]
Cottidae, genus and species undetermined [cod]
cf. Agonidae, genus and species undetermined [poacher fish]
Serranidae, genus and species undetermined [sea bass]
Carangidae, genus and species undetermined [jacks]
cf. Sparidae, genus and species undetermined [porgy]
Oplegnathidae, genus and species undetermined [knife-jaw]
Semicossyphus sp. [sheep-head]
Anarhichadidae, genus and species undetermined [wolf eel]
Thyrsocles sp. [extinct knife fish]
Scombridae, genus and species undetermined [mackerel or tuna]
Xiphiidae, genus and species undetermined [sword fish]
Paralichthys sp. [flatfish]
Pleuronectidae, genus and species undetermined [flounder]
Diodontidae, genus and species undetermined [puffer fish]
Puffinus tedfordi Howard, 1971 [extinct shearwater]
Puffinus sp. [shearwater]
Morus sp. [gannet]
?Megapaloelodus opsigonus Brodkorb, 1961 [flamingo]
Cerorhinca minor Howard, 1971 [rhinoceros auklet]
?Endomychura sp. [auklet]
Mancalla cedrosensis Howard, 1971 [flightless auk]
Thalassoleon mexicanus Repenning and Tedford, 1977 [primitive sea lion]
Dusignathinae, genus and species undetermined (identified as *Dusignathus santacruzensis*) Kellogg, 1927, by Repenning and Tedford, 1977) ["pseudo-walrus"]
Aivukus cedrosensis Repenning and Tedford, 1977 [primitive walrus]
aff. *Hydrodamalis* sp. [extinct relative of Steller's sea cow]
Dugongidae, genus and species undetermined [small sea cow]
aff. *Nannocetus* Kellogg, 1929 [small cetotheriid mysticete]
cf. *Herpetocetus* Van Beneden, 1872 [small cetotheriid mysticete]
Balaenopteridae, genus and species undetermined A [small rorquallike balaenopterid]
Balaenopteridae, genus and species undetermined B [medium-sized rorquallike balaenopterid]
Balaenopteridae, genus and species undetermined C [large rorquallike balaenopterid]
?Balaenidae, genus and species undetermined [right whale]
Parapontoporia pacifica Barnes, 1984a [pontoporiid dolphin, or "franciscana"]
Albireo whistleri Barnes, 1984a [extinct delphinoid]
Denebola brachycephala Barnes, 1984a [broad-headed belugalike monodontid]
Denebola sp. [extinct broad-headed belugalike monodontid]
Piscolithax tedfordi Barnes, 1984a [primitive phocoenid porpoise]
Piscolithax boreios Barnes, 1984a [primitive phocoenid porpoise]
Delphinoidea, family, genus, and species undetermined [unidentified dolphin]
Praekogia cedrosensis Barnes, 1973 [pygmy sperm whale]
Physeteridae, genus and species undetermined [giant sperm whale]

Table 2 Measurements (mm) of the holotypic cranium of *Albireo whistleri* Barnes, 1984a, UCMP 314589, from the Lower Member of the Almejas Formation, latest Miocene, on Isla Cedros, Baja California, Mexico; parentheses indicate estimated measurements.

Condylobasal length	(488)
Length of rostrum	(245)
Length of tooth row	(222)
Width of rostrum at base	115
Width of rostrum at mid-length	64
Width of premaxillae at rostral midlength	40
Distance from tip of rostrum to nares	(322)
Greatest preorbital width	185
Greatest postorbital width	218
Least supraorbital width	187
Greatest width of external nares	60
Greatest width of internal nares	70
Greatest width across posterior parts of premaxillae	120
Zygomatic width	227
Greatest parietal width, within temporal fossae	177
Width across occipital condyles	94
Width of foramen magnum	33
Height of foramen magnum	37
Vertical external height of braincase	139
Internal anteroposterior length of endocranial cavity	142
Anteroposterior length of temporal fossa	127
Dorsoventral height of temporal fossa	69
Anteroposterior length of bony orbit	66
Greatest length of left pterygoid	(72)

foramen relatively large and occupying approximately one third of the length of the dentary, midpart of ventral margin of dentary concave dorsally; teeth of medium size, having conical crowns and single roots with crowns curving lingually, interalveolar septa fully formed between mandibular teeth; petrosal with large foramen centrale, large posterior articular facet for tympanic bulla that is concave and nearly smooth; tympanic bulla with thick and rugose medial part of involucrum; basihyoid and thyrohyoid bones relatively large and wide; cervical vertebrae anteroposteriorly compressed; anterior rib transversely very wide and anteroposteriorly thin; manubrium relatively large; humerus, radius, and ulna all relatively short and anteroposteriorly expanded at distal ends.

Table 3 Measurements (mm) of the holotypic right dentary of *Albireo whistleri* Barnes, 1984a, UCMP 314589, from the Lower Member of the Almejas Formation, latest Miocene, on Isla Cedros, Baja California, Mexico; parentheses indicate estimated measurements.

Total length of dentary	(417)
Length of tooth row	(227)
Length of mandibular symphysis	111
Maximum height of mandibular symphysis	26
Length of mandibular foramen	128
Height of mandibular foramen	71
Height of dentary at apex of coronoid process	92
Transverse width of mandibular condyle	26

Albireo whistleri Barnes, 1984a
Figures 4–16, 17a,b,d, 18–30, 31d–f, 32b; Tables 2–4

Albireo whistleri Barnes, 1984a:31, fig. 10g and 10h, 11–13, tables 6 and 7, 1988a, 1988c, 1992a:155, 160, fig. 7, 1998:43, table 5, 2002c:163, 187, figs. 8, 11g, 11h; Folkens et al., 1989; Fordyce and Barnes, 1994:439, fig. 2b; Fordyce et al., 1995:fig. 3b; Berta and Sumich, 1999:fig. 4.30; Fordyce, 2002:463, fig. 9D.

DIAGNOSIS OF SPECIES. A species of *Albireo* differing from *A. savagei*, sp. nov., by having proportionally and absolutely smaller atlas vertebra, atlas vertebra proportionally more elongate anteroposteriorly, with shorter transverse process, smaller neural canal, and more fully formed remnant of transverse foramen; thoracic vertebrae proportionally and absolutely more compressed anteroposteriorly; first rib longer and transversely narrower, ribs having lesser arc of curvature, indicating smaller capacity thoracic cavity; additional probably species-diagnostic characters: mesorostral groove covered by premaxillae dorsally on posterior three fourths of rostrum, large-diameter bony nares, bony nares circular in cross section, cervical vertebrae 2 and 3 fused together, anterior palatine foramen lacking, posterior palatine foramen small and located near palatine–pterygoid suture, petrosal with relatively small and globular anterior process.

HOLOTYPE. UCMP 314589 (formerly UCR 14589), a nearly complete skeleton including the cranium, both petrosals, both tympanic bullae, auditory ossicles, mandible with teeth in place, isolated teeth, nearly complete postcranial skeleton; lacking only the posterior lumbar vertebrae, all of the caudal vertebrae, and some of the phalanges; collected by David P. Whistler and George T. Jefferson, 15 July 1964.

TYPE LOCALITY. UCR locality RV-7309, in "Arroyo Delfin," from Unit 6 (stratigraphically correlated with Unit F) in the lower part of the Lower Member of the Almejas Formation (Fig. 2), on an east-facing erosional slope in the eroded badlands south of the village of Cedros, near the southeast corner of Isla Cedros, Baja California, Mexico (Fig. 1). Although from a different locality, this is in the same stratigraphic level in the Lower Member of the Almejas Formation that produced the holotypes of the broad-headed belugalike monodontid *Denebola brachycephala* Barnes, 1984a, and the primitive

Table 4 Comparative measurements (mm) of vertebrae of two species of *Albireo*: the holotype of *A. whistleri* Barnes, 1984a, UCMP 314589, from the Lower Member of the Almejas Formation, latest Miocene, on Isla Cedros, Baja California, Mexico, and the holotype of *A. savagei*, sp. nov., UCMP 112048, from the Squire Member of the Pismo Formation, late Pliocene, at Avila Beach, San Luis Obispo County, California, USA. Parentheses indicate estimated measurements.

	Albireo whistleri	*Albireo savagei*
Anteroposterior thickness of atlas vertebra through left articular surfaces	29	30
Greatest transverse width of atlas vertebra	(148)	158
Greatest dorsoventral height of atlas vertebra	(87)	96
Height of neural canal of atlas vertebra	48	59
Anteroposterior length of fourth thoracic vertebra centrum	(24)	26
Anteroposterior length of fifth thoracic vertebra centrum	(25)	31
Anteroposterior length of sixth thoracic vertebra centrum	(30)	—
Anteroposterior length of seventh thoracic vertebra centrum	(31)	38
Anteroposterior length of eighth thoracic vertebra centrum	(31)	8
Anteroposterior length of 11th thoracic vertebra centrum	39	
Anteroposterior length of possible 11th thoracic vertebra centrum		43

phocoenid porpoise *Piscolithax tedfordi* Barnes, 1984a.

REFERRED SPECIMEN. UCMP 324043, incomplete right tympanic bulla, collected by Richard H. Tedford and party, 11 August 1965, field number RHT 1312c.

LOCALITY OF REFERRED SPECIMEN. UCR locality RV-7304, Richard H. Tedford Field Locality 1, specimen found lying loose on the surface of Unit 10 (stratigraphically correlated with Unit J) of the Lower Member of the Almejas Formation, approximately 40–60 feet (~12–18 m) above the base of the Almejas Formation (Fig. 2), in south-facing badlands south of the village of Cedros, near the southeast corner of Isla Cedros, Baja California, Mexico. This is the same locality and stratigraphic horizon that yielded an isolated petrosal (UCMP 321247, formerly UCR 21247) of a large physeterine sperm whale (see Barnes, 1984a:41, fig. 15). Because this specimen was discovered lying loose on the surface of Unit 10, approximately 30 to 40 feet (~9–12 m) stratigraphically above the occurrence of the holotype of *A. whistleri*, it could have been derived from a higher stratum.

FORMATION AND AGE. *Albireo whistleri* is known only from the Lower Member (as defined by Kilmer, 1977, 1979) of the Almejas Formation (as defined by Mina, 1957), of latest Miocene age, approximately 6 to 8 Ma, correlative with the Jacalitos and/or the later part of the Etchegoin provincial invertebrate stages of Addicott (1972) (see Barnes, 1972, 1973, 1977:331, fig. 2, 1984a, 1985b, 1997b, 1998). The invertebrate fossils from the Almejas Formation that were described as Pliocene in age by Hertlein (1925) and by Jordan and Hertlein (1926) are from the overlying Upper Member (as defined by Kilmer, 1977) of the Almejas Formation. Thus the invertebrate fossils help to constrain the age of the vertebrate-bearing Lower Member of the formation (Fig. 2) and to place a minimum age on its fossils, but they are not directly relevant to determining the geochronologic age of the Lower Member.

Albireo whistleri is part of the most diverse and best preserved post–middle Miocene assemblage of fossil marine vertebrates that has yet been described from the Pacific coast of North America. This assemblage (Table 1) from the Lower Member of the Almejas Formation includes at least 61 species of elasmobranchs, bony fishes, birds (Howard, 1971), pinnipeds (Repenning and Tedford, 1977), cetaceans (Barnes, 1971, 1973, 1977, 1984a, 1991, 1992a, 1992b, 1992c, 1997b, 2002c), and sirenians. The fossil specimens that document this assemblage are conserved in the Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico; Universidad Nacional Autónoma de México in Mexico City, Mexico; the UCMP; and the LACM.

The fossil vertebrae faunal assemblage from the Lower Member of the Almejas Formation is presently known to include the taxa that are listed in Table 1. Identifications of the sharks (Table 1) are based in part on identifications by the late Shelton P. Applegate, Francisco J. Aranda-Manteca, Gerardo González-Barba, and J.D. Stewart (1997). The teeth of the giant shark *Carcharocles megalodon* (Agassiz, 1843) in the collections are not eroded and appear not to have been reworked from an older deposit. Teeth of the smaller great white shark, *Carcharodon* cf. *C. carcharias* (Linnaeus, 1758), are more abundant in the deposit, and they closely resemble teeth of *Isurus hastalis* Agassiz, 1843, in shape. The co-occurrence of *C. megalodon* and *Carcharodon* cf. *C. carcharias* has been documented in other latest Miocene eastern Pacific assemblages, including those from the San Mateo Formation (see Barnes et al., 1981) and the Capistrano and Purisima formations in California (Stewart and Perry,

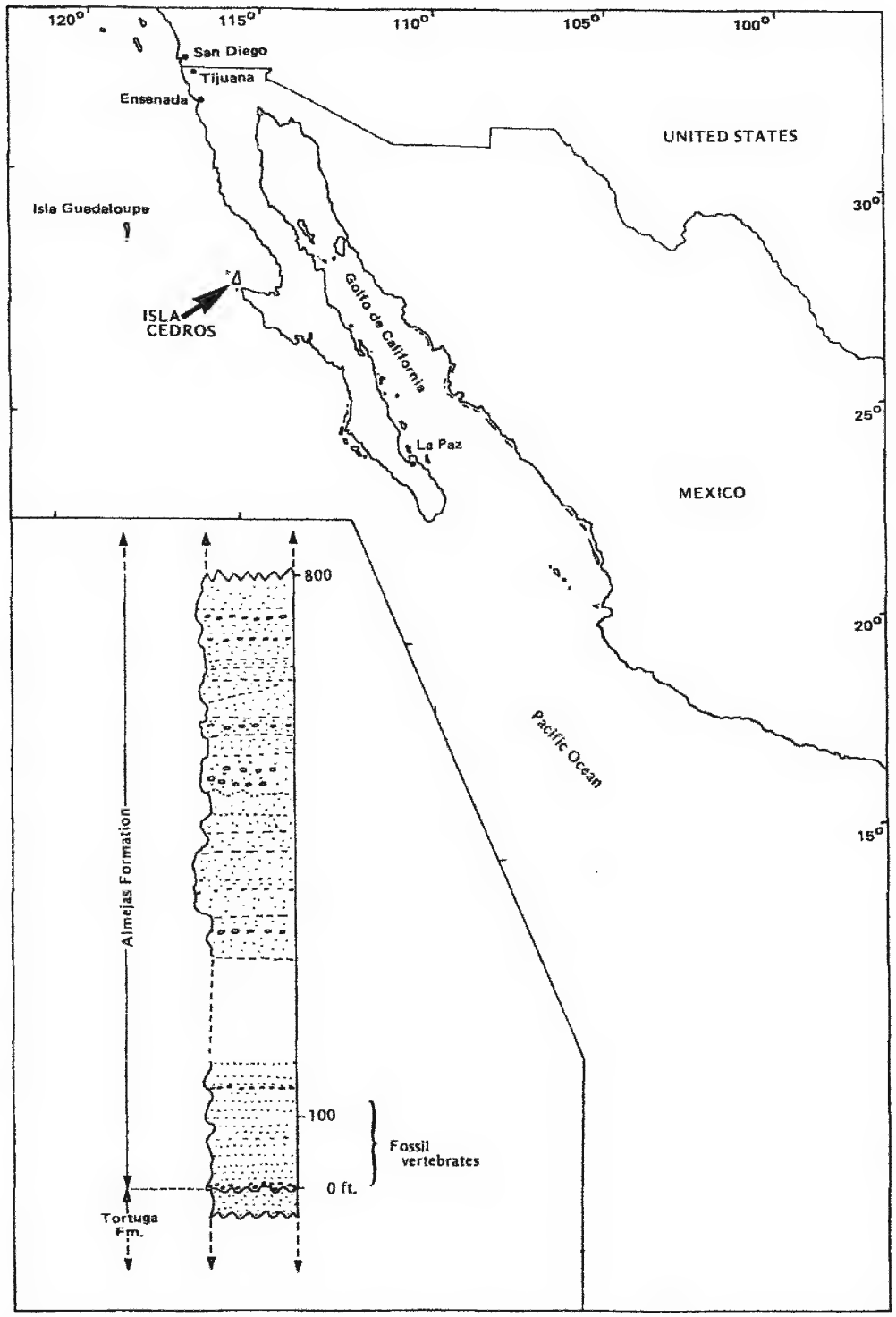

Figure 1 Map showing location of Isla Cedros, in the eastern North Pacific Ocean, along the west coast of Baja California, Mexico. Inset: generalized stratigraphic column of strata that are exposed at the southeast corner of Isla Cedros, where the Almejas Formation of latest Miocene and Pliocene age unconformably overlies the middle Miocene Tortuga Formation. The Lower Member of the Almejas Formation, which yielded the holotype of *Albireo whistleri* and other marine vertebrate fossils, is indicated by the section labeled "Fossil vertebrates." (Inset from Field Notes of Richard H. Tedford, data from Kilmer [1977, 1979], Repenning and Tedford [1977], and Barnes [1984a, 1992a]).

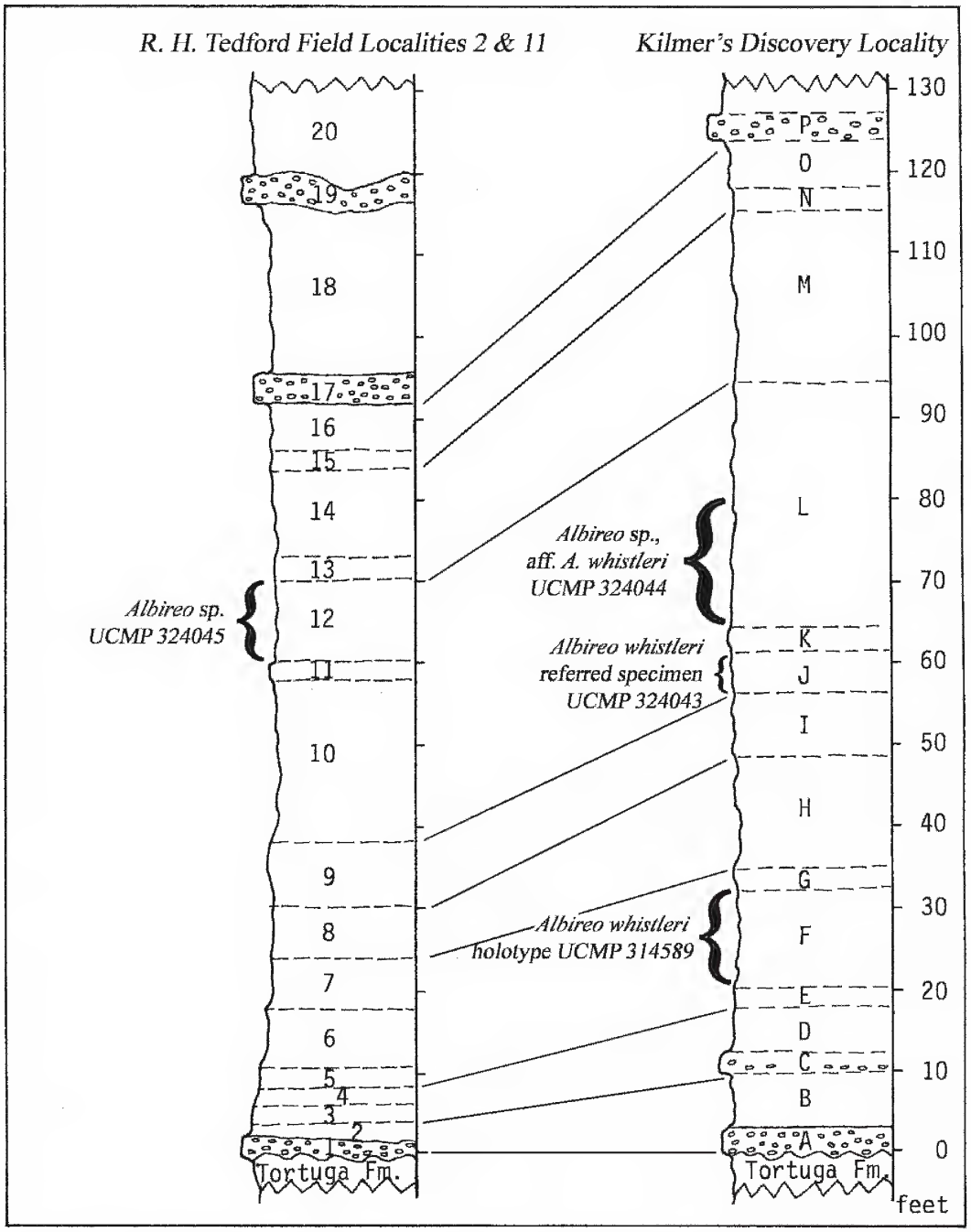

Figure 2 The stratigraphic position of the holotype of *Albireo whistleri* Barnes, 1984a (UCMP 314589), and other related taxa within the latest Miocene age Lower Member of the Almejas Formation on Isla de Cedros, Baja California, Mexico. These two stratigraphic columns were made by Richard H. Tedford and party in 1965, are modified from the field notes of Tedford for that expedition, and incorporate new information (e.g., Barnes and González-Barba, 1993; Aranda-Manteca and Barnes, 1995; Barnes et al., 1997). In subsequent field work, the correlations that were suggested by Tedford were found to be so precise, and the strata were found to be so laterally continuous, that only the system of numbered beds has been used subsequently, and the lettered sequence of beds has been discontinued.

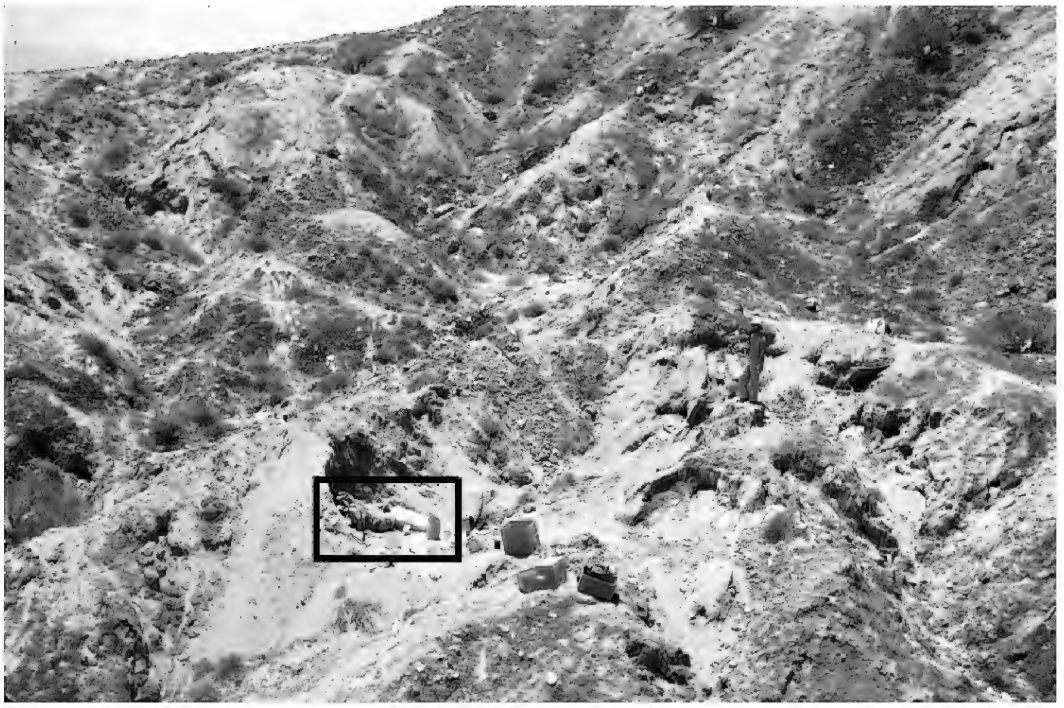

Figure 3 Discovery site (UCR RV-7309, outlined in the black box) of the holotype (UCMP 314589), of *Albireo whistleri* Barnes, 1984a, in the ravine that was named in 1964 and 1965 "Arroyo Delfin," at the southeast corner of Isla Cedros, Baja California, Mexico. Here, locality UCR RV-7309 is located in exposures of Unit 6 (= Unit F) in the latest Miocene age basal part of the Lower Member of the Almejas Formation. A member of the field party observes the site from across the arroyo. (Photograph by David P. Whistler, 15 July 1964.)

2002), both of which are latest Miocene to early Pliocene (Hemphillian correlative) rock units, and also from "Pliocene" rocks near Sacaco, Peru (Muizon and DeVries, 1985). Identifications of the birds, with the exception of the change in family assignment of the flamingo, follow Howard (1971). The classification of the pinnipeds is based partly on the work of Repenning and Tedford (1977), with additions and modifications. The pygmy sperm whale, *Praekogia cedrosensis*, was described by Barnes (1973), and it and seven other odontocete species were reported in other studies (Barnes, 1971, 1972, 1977, 1984a, 1985a, 1985b). The mysticete whales have not yet been precisely identified, but their diversity has been reported by Barnes (1972, 1977, 1992a, 1992c, 1998, 2002c) and by Gascón-Romero et al. (1997).

DESCRIPTION. General Morphology. The cranium, mandible, and petrosal were illustrated and described in the original description of *A. whistleri* by Barnes (1984a). Figure 4 presents the nearly complete skeleton as found at the discovery site and Figure 5 shows the position of the bones in the field plaster jacket. Additional illustrations and observations of the cranial and postcranial skeleton are provided here. Because the holotypic skeleton of *A. whistleri* is nearly complete (Fig. 6; and see Fordyce and Barnes, 1994:fig. 2b; Fordyce et al., 1995:fig. 3b; Barnes, 1998:fig. 7a, 2002c:fig. 8c), the specimen allows a relatively detailed assessment of the morphology of the animal. In life, an adult *A. whistleri* was approximately the size of living species of dolphins in the genus *Lagenorhynchus* Gray, 1846; thus, in comparison with various living delphinid species, it is a medium-sized dolphin, and it was approximately 2.5 m in total length when mature on the basis of comparisons with the vertebral column of living species of the genus *Lagenorhynchus*. The distal extremities of both the rostrum and the mandible were slightly curved dorsally.

Derived characters of the species include its large braincase, highly elevated cranial vertex, dorsally curved rostral extremity, large premaxillary eminences, flat nasal bones, anteroposteriorly compressed vertebrae, very slender and elongate neural and transverse processes of the dorsal vertebrae, and very wide and flat pectoral flipper bones. Its primitive characters include a symmetrical cranial vertex, relatively simple basicranium lacking extensive fossae for air sinuses, and nonfused cervical vertebrae (except for fusion of the second and third vertebra).

Figure 4 The nearly complete holotypic skeleton (UCMP 314589) of *Albireo whistleri* Barnes, 1984a, in place during excavation at the type locality (UCR RV-7309), in Unit 6 (= Unit F) in the basal part of the Lower Member of the Almejas Formation on Isla Cedros, Baja California, Mexico. The cranium and dentaries are in the foreground, and the nearly articulated vertebral column extends behind, with the ribs lying adjacent to the vertebrae in the right side of the image. (Photograph by David P. Whistler, 15 July 1964.)

Figure 5 *Albireo whistleri* Barnes, 1984a, thoracic part of the holotypic skeleton, UCMP 314589, photographed in the laboratory while still in the field plaster jacket, to show the positions of bones prior to removal. This is the field bottom view, so the positions of the bones are reversed from those in Figure 4. The numbered paper labels on the bones have been kept in place to identify the various elements. Major bones are: 1, left scapula; 3, left ulna; 4, left radius; 5 and 6, left metacarpals associated with other bones of the left fore flipper; 8, right ulna; 14, second thoracic vertebra; 16, left first rib; 24, ninth thoracic vertebra.

Body Restoration. On the basis of all available evidence, Folkens et al. (1989) created a life reconstruction of the species, and that restoration is presented here as Figure 7. The facial region of the cranium is relatively wide, so the melon probably was comparatively large, and the forehead was probably shaped somewhat like that of Recent *Tursiops truncatus* or of the Dall's porpoise, *Phocoenoides dalli* True, 1885.

Although the cervical vertebrae are anteroposteriorly shortened, as is typical of delphinoids, only two of the vertebrae are fused, thus the neck was undoubtedly more flexible than it is in extant species of Delphinidae. The length and numbers of ribs and the height of the dorsal processes of the vertebrae indicate that the body was stout and that it was particularly deep in the thorax. Considering the height of the dorsal processes of the lumbar vertebrae, the dorsal processes of the anterior caudal vertebrae were probably also relatively high, and for this reason, the animal probably had a deep caudal peduncle.

There is no way to determine for certain the size and shape of the dorsal fin of *A. whistleri*. In fact, this species could have lacked a dorsal fin. Most living pelagic dolphins do have a fin, and in the restoration of *A. whistleri* (Fig. 7), the dorsal fin is shown as being much like that of *T. truncatus* or of the rough-toothed dolphin, *Steno bredanensis* (G. Cuvier in Lesson, 1828), but this is purely conjectural.

Because of the anteroposterior expansion of the radius and ulna, the pectoral flippers of *A. whistleri* must have been flattened transversely and broad anteroposteriorly (Fig. 7). In the restoration, the missing bones and the phalangeal formula are based on the structures of the Recent delphinids, *T. truncatus* and the common dolphin *Delphinus delphis* Linnaeus, 1758. The caudal vertebrae are missing from the holotypic skeleton, so there is no way to determine where the anterior margin of the caudal flukes would have been positioned in the tail region. The vertebrae that are present in the holotype have proportions similar to those of Recent species of *Lagenorhynchus*, and in the restoration the shape and proportions of the peduncle region and caudal flukes are patterned after species of *Lagenorhynchus*.

Cranium. The cranium of *A. whistleri* (Figs. 8 and 9) is proportionally large compared with the size of the dolphin's body. The braincase is large and rounded, and the cranial vertex is elevated and symmetrical. The facial region is steeply ascending posterior to the nares. The occipital condyles and the zygomatic processes of the squamosals are large. The rostrum is of intermediate length compared with other odontocetes, is tapered toward its extremity, and is curved dorsally at its distal end.

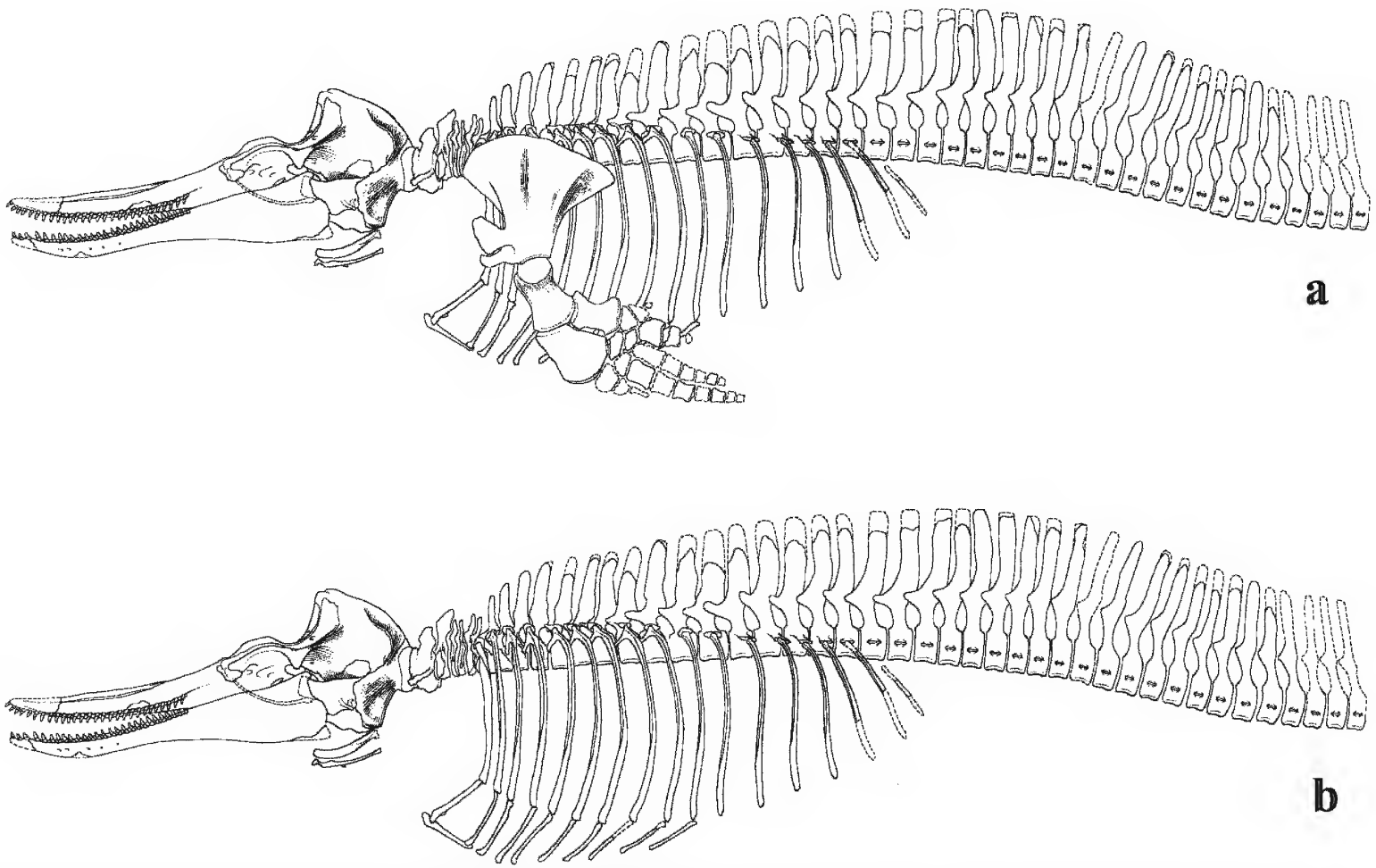

Figure 6 Reconstructions of the nearly complete holotypic skeleton, UCMP 314589, of *Albireo whistleri* Barnes, 1984a: **a**, reconstruction with the forelimb in anatomical position; **b**, reconstruction without the forelimb to show the entire thoracic region. (Artwork by Wendy Smith Griswold.)

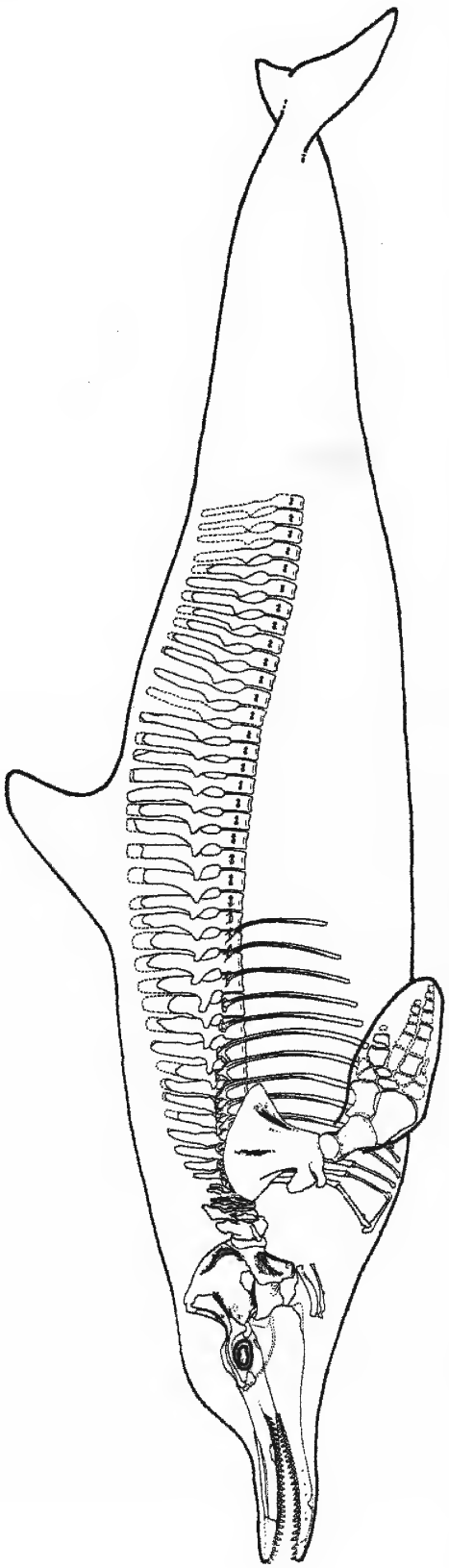

Figure 7 *Albireo whistleri* Barnes, 1984a, suggested restoration of the body shape of an adult individual in life, based on the skeletal reconstruction of the holotype shown in Figure 6a. (Reconstruction by Pieter A. Folkens.)

The mesorostral groove is closed dorsally where the premaxillae meet at the midline from the location immediately anterior to the nares to approximately three fourths of the length of the rostrum. The right and left premaxillae appear to have been separated near the anterior end of the rostrum. This is because the medial margin of the right premaxilla departs from the mesorostral groove for a distance of 35 mm, and here it has a fully formed and relatively sharp medial edge. The corresponding medial edge of the left premaxilla is incomplete, however, and the distal ends of both premaxillae are broken off. It is clear, however, that a short section of the mesorostral groove was originally exposed at the anterior tip of the rostrum

On the dorsal surface of the rostrum, the premaxillae are depressed medially. Approximately three fourths of the distance posteriorly on the rostrum is a relatively large-diameter anterior maxillary foramen along each side at the maxilla/premaxilla contact, and at this foramen is an indentation in the lateral side of the premaxilla (Fig. 10). There is a more pronounced medial constriction of the lateral margin of each premaxilla at the base of the rostrum between the antorbital notches. In this area of constriction of the premaxillae, on each side are three additional small anterior maxillary foramina along the premaxilla/maxilla suture. Dorsal to the orbit are three or four more anterior maxillary foramina along the posterior parts of both of the premaxillary/maxillary sutures. These foramina that are scattered along the premaxillary/maxillary sutures are an apomorphy of *A. whistleri.*

A premaxillary eminence is located anterior to each naris. Each premaxillary eminence is low, relatively narrow, smoothly rounded, and highest near the midline of the cranium. Among various groups of Odontoceti, the presence of premaxillary eminences (in some literature referred to as premaxillary bosses) is a derived but convergent character. The premaxillary eminences in phocoenids are sites of attachment for the nasal plug muscles, and presumably this was also the case in *A. whistleri.* Premaxillary eminences are among the diagnostic characters of the Phocoenidae (Barnes, 1985a).

Other types of premaxillary eminences are present in various other species of odontocetes—for example, in species of the families Pontoporiidae, Iniidae, and Ziphiidae. Therefore, it is not the presence or absence of these eminences that is of phylogenetic significance among odontocetes; rather, it is their location and the details of their structure that are significant. For example, among the Phocoenidae, these eminences are elevated abruptly from the surrounding bone, are flat to slightly convex on their dorsal surface, and have a well-defined lateral margin that is formed in part by the presence of the posterolateral sulcus which is connected to the premaxillary foramen. In *A. whistleri*, however, the eminences have a longitudinal crest at their apices, and they slope smoothly onto the surfaces of the surrounding bone on all sides.

The posterior parts of the premaxillae of *A. whistleri* are not developed into raised premaxillary sac fossae as is typically the case in odontocetes—for example, in members of such families as the Eurhinodelphinidae, Kentriodontidae, and Delphinidae. Instead, the posterior parts of the premaxillae are transversely widened, flat dorsally, thin, and slightly concave, and they extend farther posteriorly than the posterior margins of the nasal openings (Figs. 10 and 11). The widening of the posterior ends of the premaxillae of *A. whistleri* is autapomorphic compared with other Odontoceti.

The structure of the posterior ends of the premaxillae indicates that, in life, a large premaxillary sac was located lateral to each naris. Odontoceti typically have premaxillary sac fossae, but their locations on the premaxillae are in most species on raised areas of bone. The premaxillary sacs are diverticulae of the dorsal narial passages, and they have a function in sound production (Norris, 1968; Norris and Harvey, 1972; Mead, 1975; Au, 2002). In *A. whistleri*, the flatness of the premaxillary sac fossa areas and the relatively dense surface texture of the premaxillary bone suggest that the premaxillary sacs were relatively larger than is typical for most delphinoids.

The narial passages pass nearly vertically through the cranium; they do not curve around the anterior side of the braincase as they do in some odontocetes. As with other derived species of delphinoids, *A. whistleri* has no olfactory foramina on the posterior walls of the nares. The bony posterior wall of each narial passage is continuous as it exits from the cranium. In typical odontocetes, the nasal bones contact the mesethmoid in a transverse suture across the posterior wall of the narial passages. In *A. whistleri*, the ethmoid bones do not come into contact with the nasal bones. Instead, there is a transverse band of exposure of the underlying frontal bones that makes a surface appearance, and which separates the ventral edge of each nasal bone from the dorsal margin of the mesethmoid bone. This exposure of the frontal bones on the posterior wall of the narial passages is an autapomorphy of the family Albireonidae.

The nasal bones are wide and very flat, and they have irregular borders. The extreme flatness and thinness of the nasal bones of this species is a unique character among known odontocetes. Because the nasal bones are inclined on the sloping surface of the facial region and are not positioned at the top of the cranial vertex as they are in other delphinoids, the dorsal view of the

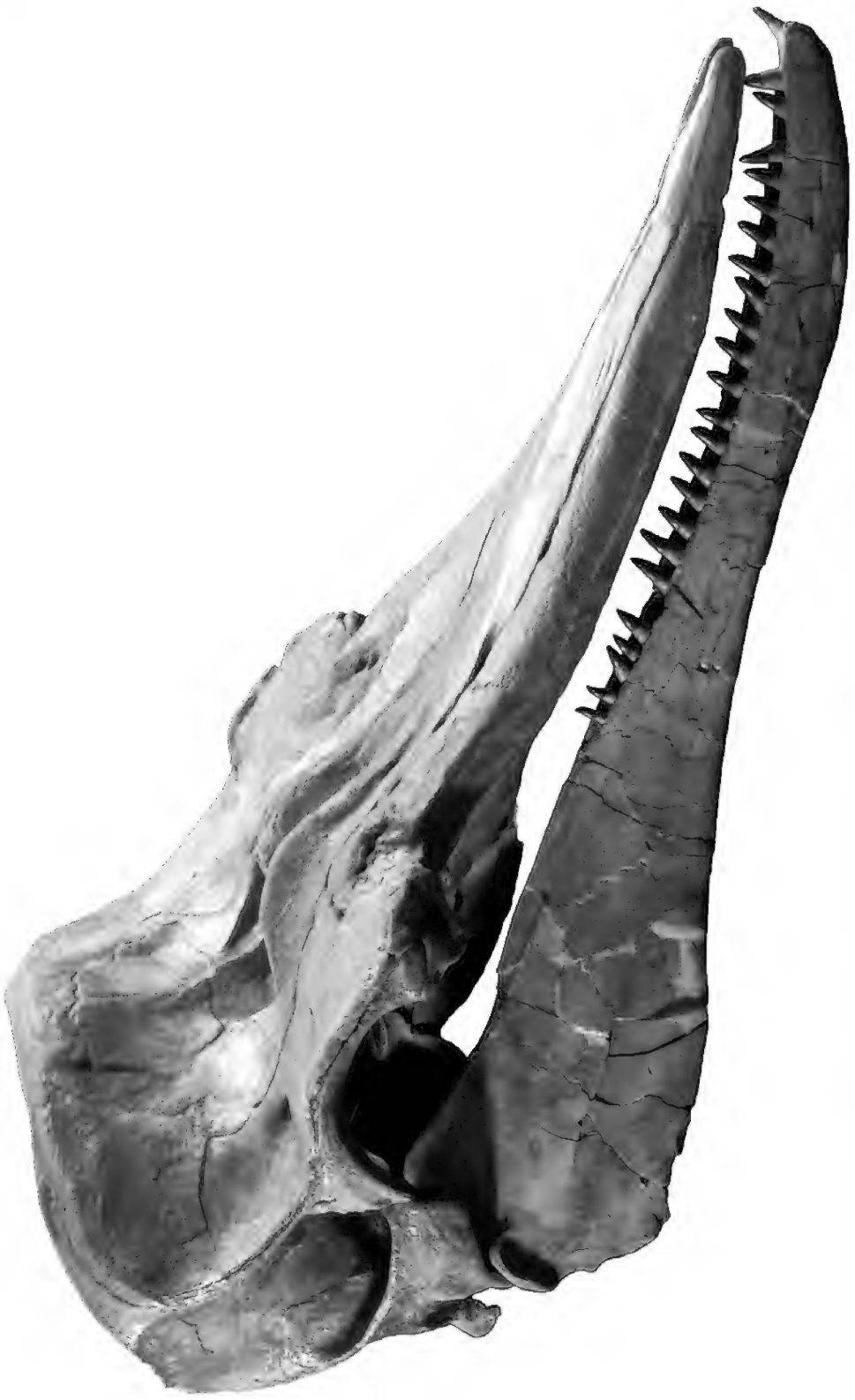

Figure 8 *Albireo whistleri* Barnes, 1984a, holotypic cranium and mandible, UCMP 314589, in oblique right lateral view.

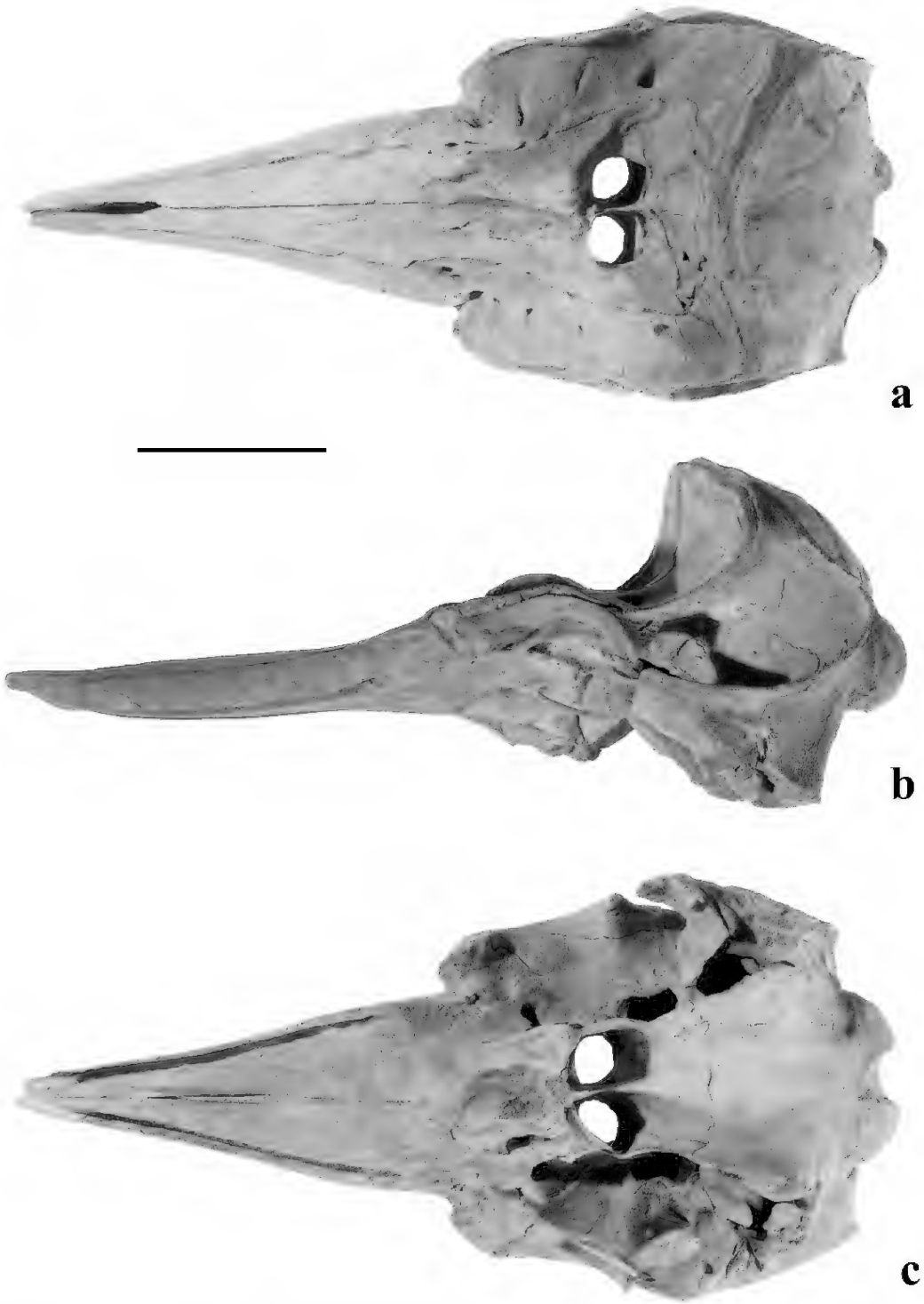

Figure 9 *Albireo whistleri* Barnes, 1984a, holotypic cranium, UCMP 314589: **a**, dorsal view; **b**, left lateral view; **c**, ventral view. Scale bar = 10 cm.

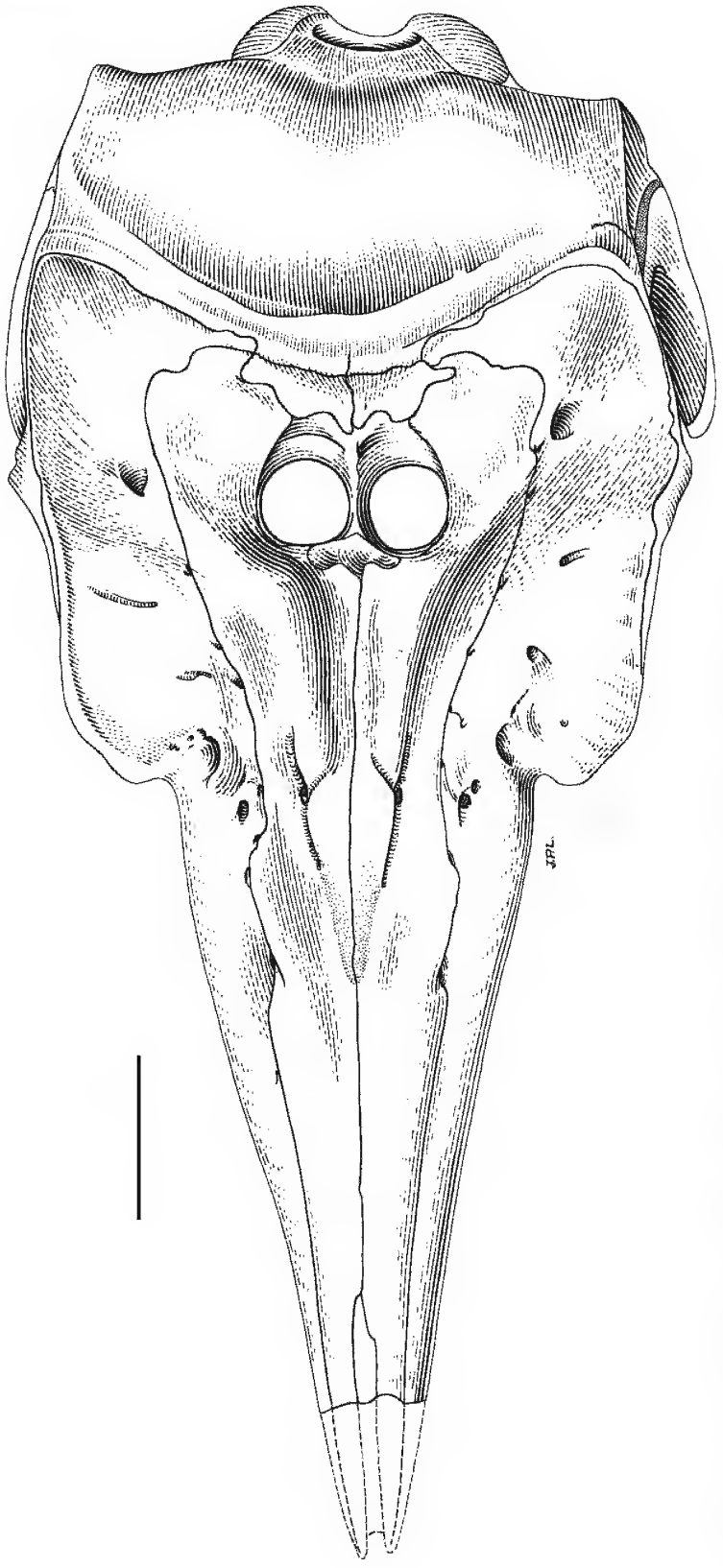

Figure 10 *Albireo whistleri* Barnes, 1984a, holotypic cranium, UCMP 314589, dorsal view. Scale bar = 5 cm.

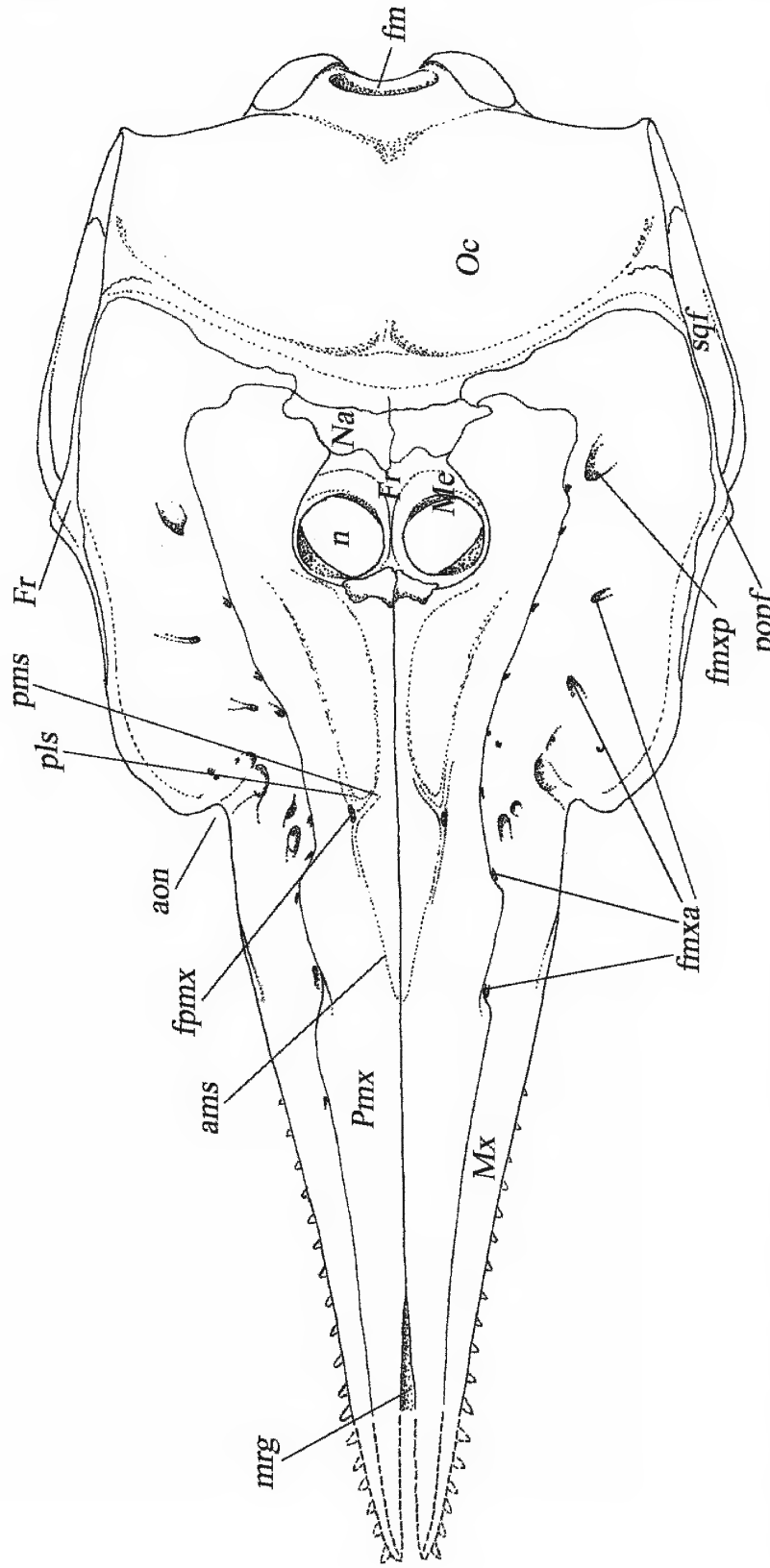

Figure 11 *Albireo whistleri* Barnes, 1984a, holotypic cranium, UCMP 314589, dorsal view restored with parts labeled. See "Methods and Materials" for abbreviations.

cranium does not provide an accurate view of their shapes. Each nasal bone has a notch in its anterior margin and a prolongation at both the anteromedial corner and on the lateral side. The posterior margin of each nasal bone is nearly straight transversely. The premaxillae extend posteriorly to the posterolateral corner of each nasal bone (see Fig. 11). Neither the posterior ends of the premaxillae, nor the contacts that they have with the nasal bones, are bilaterally symmetrical. However, this asymmetry does not involve any skew to either the right or left side of the sagittal plane. Neither the cranial vertex nor the narial region is skewed to the left, as is typical of species of the Delphinidae and of many other odontocete families.

The curious, extreme flattening of the posterior ends of the premaxillae, the nasals, and the frontals around the nares, however, are autapomorphies of *A. whistleri* that are not found in other odontocetes. In other odontocetes, these bones are elevated above the surrounding maxillae.

As is typical of delphinoids, the frontals unquestionably contribute to the cranial vertex, but because of the maturity of the holotypic individual, the sutures between the frontals, parietals, and supraoccipital on the cranial vertex are fused and are obliterated. The margins around the posterior ends of the maxillae are clearly recognizable, and they do not quite reach the nuchal crest, which is that structure being formed by the fused and obliterated sutures between a transverse band of the frontals and the supraoccipital.

The temporal fossa is relatively large. Unlike that of most Recent species of the family Delphinidae, it is not circular in lateral view, but it is narrow anteriorly and wider posterodorsally (see Figs. 12 and 13). Most of the temporal fossa is not visible in the dorsal view of the cranium because the frontal and maxilla extend laterally over it.

Because of the maturity of the holotypic specimen, the bones composing the occipital shield had become fused and cannot be individually distinguished. The occipital shield is transversely broad and has an almost uniformly convex surface. There is a slight concavity in its dorsal part ventral to the nuchal crest. The lambdoidal crests are most clearly formed only around the ventral part of the posterior margin of the temporal fossae. More dorsally, approaching the top of the temporal fossae, the lambdoidal crests are indistinct, and the occipital shield merges smoothly with the posterior part of the temporal fossa (Fig. 12). The occipital condyles are large, and they are demarcated around their dorsal margins by transversely widened supracondylar fossae. The ventral margins of the condyles are transversely broad, and they are not noticeably separated from the ventral surface of the basioccipital.

The palatal surface of the rostrum is relatively featureless, and it is generally slightly convex. The anterior part of the palate is concave along its midline, where there is an elongate and narrow ventral exposure of the vomer bone. This exposure of the vomer is flanked in its anterior part by the premaxillae, which extend anteriorly to ultimately occupy all of the palatal surface (Figs. 14 and 15). The palatal exposure of each premaxilla extends posteriorly almost as far as one third of the exposed vomer. This extensive palatal exposure of the premaxilla is greater than is typical among Odontoceti, and it is greater than it is in most species of Delphinoidea. In species of the Delphinidae, for example, the premaxillae are exposed only on the anteriormost part of the palate, and they do not contact the vomer bone, which in many delphinid species does not have any exposure on the palate. In species of Monodontidae and Phocoenidae, the premaxilla extends posteriorly, and it only contacts the anteriormost part of the exposed vomer.

The elliptical palatal exposure of the vomer as it exists in *A. whistleri* is probably a primitive character state among the Delphinoidea, even though it is not a primitive character state for Cetacea. The exposure of the vomer is present in various species of the Kentriodontidae, such as the kentriodontine kentriodontid genus *Kentriodon* Kellogg, 1927 (see Barnes and Mitchell, 1984: fig.14), the kentriodontine kentriodontid *Macrokentriodon morani* (see Dawson, 1996b:fig. 1b), the lophocetine kentriodontid *Hadrodelphis calvertense* (see Dawson, 1996a:fig. 1b), and the lophocetine kentriodontid *Lophocetus repenningi* (see Barnes, 1978:figs. 8 and 9).

In contrast, the extensive contact on the palate between the premaxilla and the anterior one third of the exposed vomer is apparently a derived character of *A. whistleri.* This is because, among the kentriodontids cited above, the premaxilla makes no such contact with the vomer in species of *Kentriodon*, and it makes only a very small contact in *M. morani* and in *H. calvertense.*

On the posterior part of the palate, each palatine bone is exposed in a broad U-shaped area around the posterior end of each maxilla. The maxillae are exposed in narrow V-shaped areas that extend posteriorly between the palatines.

Extensive development of cranial air sinuses in Odontoceti is usually either correlated with or attributed to the ability to pressure regulate during deep dives and/or with the provision of a shield that isolates the brain and/or the ear regions from echolocation sounds (Norris, 1968; Norris and Harvey, 1972; Barnes, 1984b). Compared with Recent species of the Delphinidae

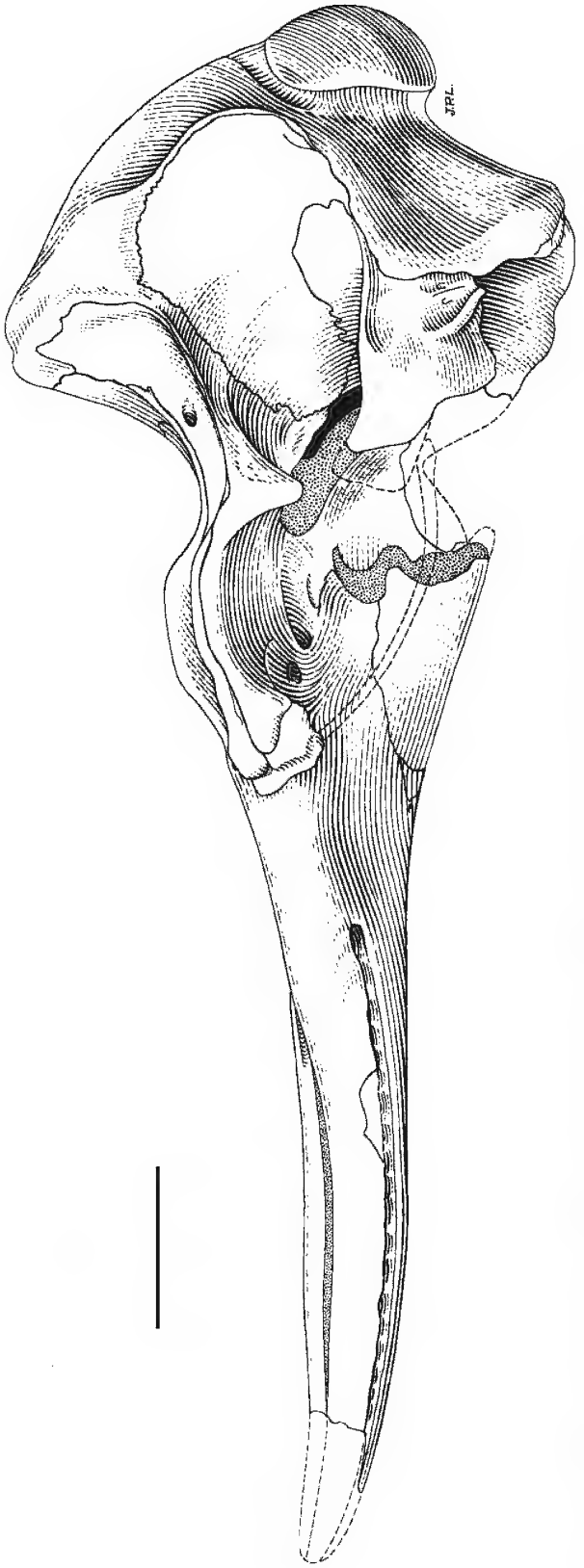

Figure 12 *Albireo whistleri* Barnes, 1984a, holotypic cranium, UCMP 314589, left lateral view. Scale bar = 5 cm.

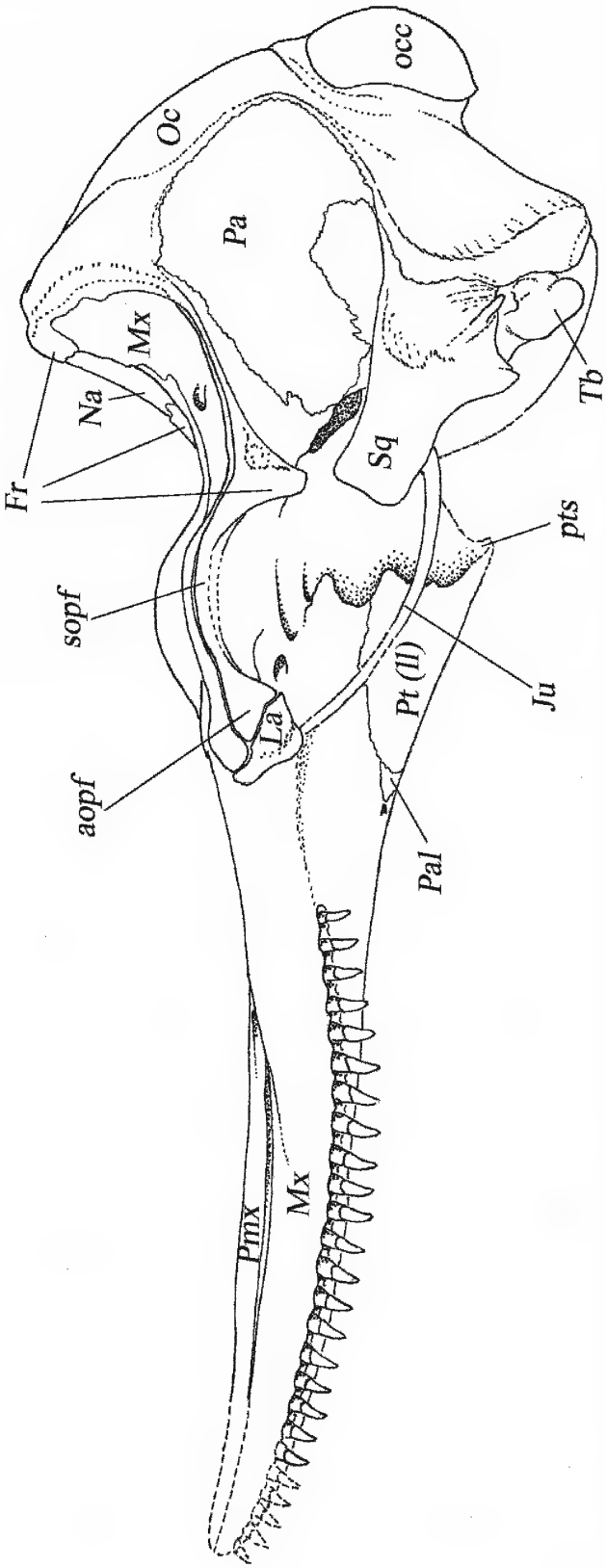

Figure 13 *Albireo whistleri* Barnes, 1984a, holotypic cranium and left dentary, UCMP 314589, left lateral view restored with parts labeled. See "Methods and Materials" for abbreviations.

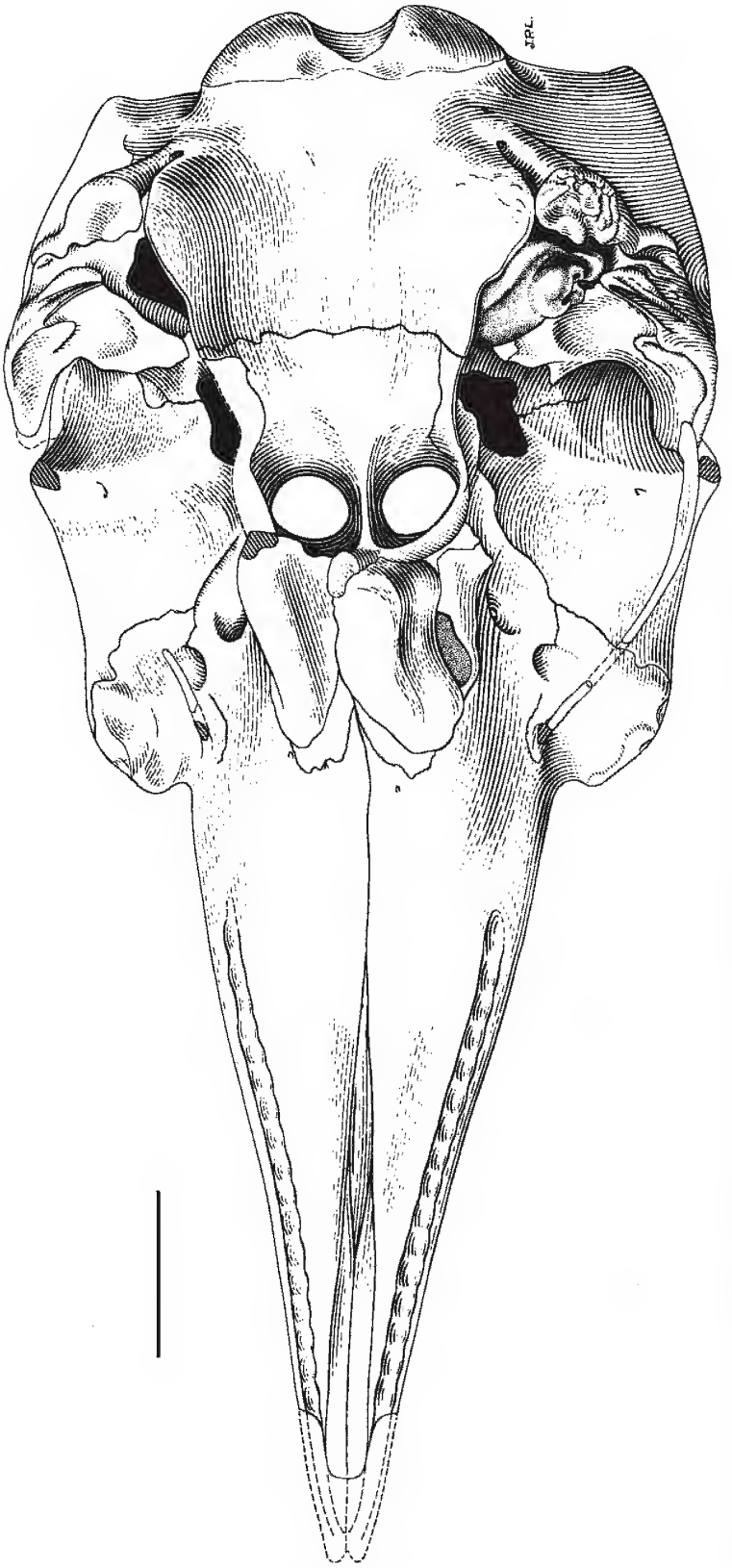

Figure 14 *Albireo whistleri* Barnes, 1984a, holotypic cranium, UCMP 314589, ventral view. Scale bar = 5 cm.

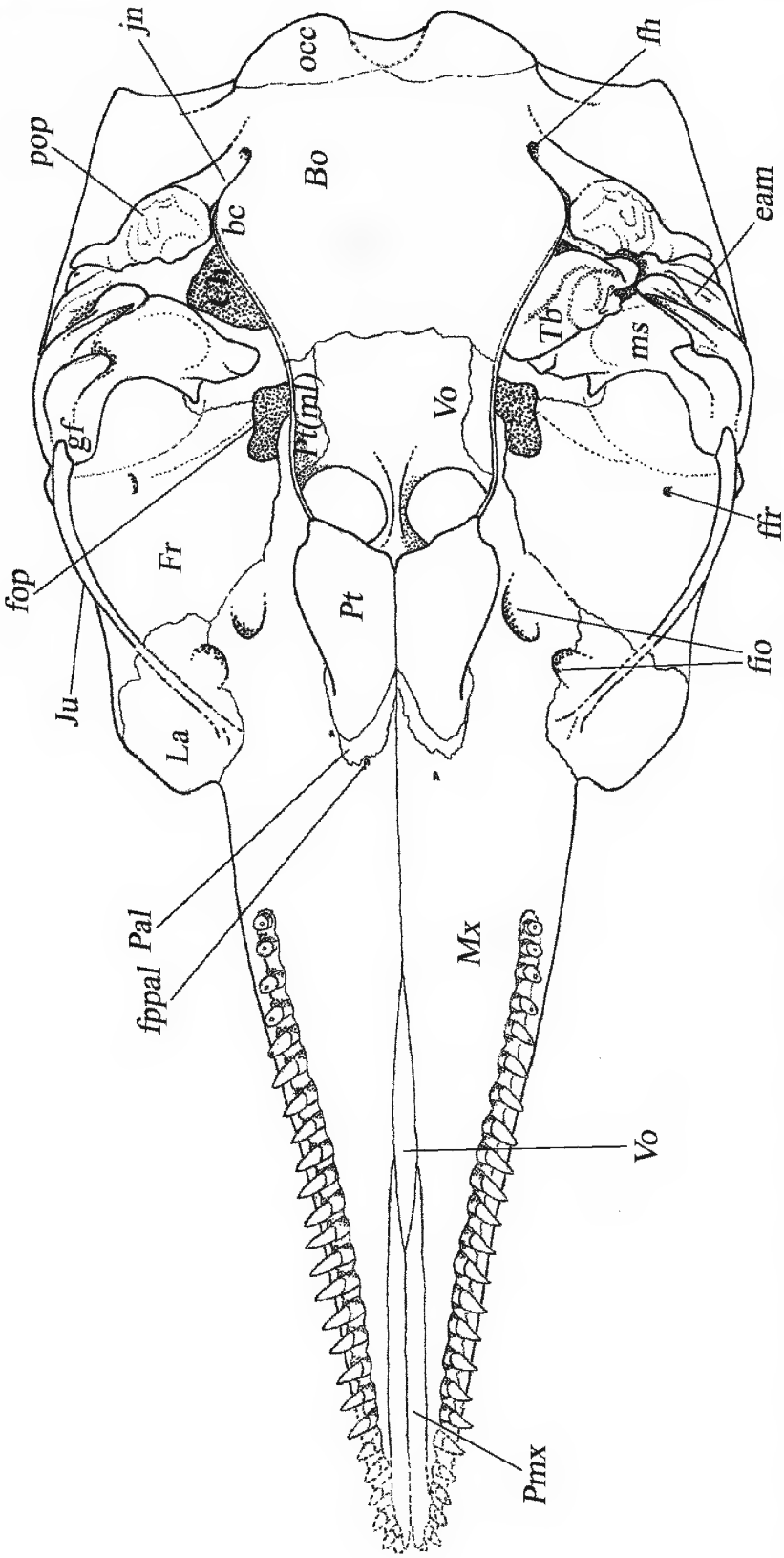

Figure 15 *Albireo whistleri* Barnes, 1984a, holotypic cranium, UCMP 314589, ventral view restored with parts labeled. See "Methods and Materials" for abbreviations.

and Phocoenidae, *A. whistleri* has a lesser degree of development of fossae in the basicranium that in life would have accommodated sinuses of the middle ear air sinus. Its cranium only has fossae that would have contained the peribullary, posterior, middle, and pterygoid sinuses (e.g., Fraser and Purves, 1960). These four sinuses are present in and diagnostic for all Odontoceti.

The orbit is remarkably devoid of any fossae in the bones that would indicate the presence in life of antorbital or postorbital lobes of the pterygoid sinus, both of which occur in various delphinoids. *Albireo whistleri* lacks any fossa or sulcus on the posterolateral parts of the palate that would have held an enlarged anterior sinus. Furthermore, no fossa extends posterodorsally from the orbit between the frontal and maxilla that would have held a branch of the pterygoid sinus, a sinus that is typically present in species of the Phocoenidae and is diagnostic of that family (Barnes, 1985a). There are no fossae in the lateral side of the basioccipital that would indicate the presence of any air sinuses that would have extended from the peribullary sinus. Such a sinus in the lateral side of the basioccipital is also present in species of Phocoenidae. There is no fossa for a posterior sinus in the area of the jugular notch. As is typical of all species of Delphinoidea, the middle sinus was relatively large, as indicated by a fossa (the tympanosquamosal recess) in the ventral surface of the squamosal medial to the glenoid fossa.

The pterygoid sinuses are relatively large; they invade virtually all of the palatal portions of the pterygoid bone, and they are enclosed ventrally and laterally by very thin pterygoid bone. The right and left pterygoids meet medially; thus, the pterygoid sinuses are close together at the posterior end of the palate. As is typical of delphinoids, the pterygoid sinus is open both laterally and posteriorly, with a lateral-facing aperture that extends posteriorly, facing toward the ventral narial openings.

There is no evidence of a "reduplicated pterygoid" (*sensu* Miller, 1923) or of any other kind of ossified wall within the orbit. The optic foramen is a large, irregularly shaped opening into the braincase. The ventral surface of the supraorbital process of the maxilla is wide, smooth, and featureless, except for a small frontal foramen near the base of the postorbital process of the frontal.

There is a very small diameter carotid canal in the lateral side of the basioccipital. The cranial hiatus is of large size, and the petrosal and bulla were undoubtedly surrounded in life by a large peribullary sinus. The shelf of the squamosal bone that forms the roof of the fossa for the peribullary sinus extends medially at the anterior edge of the cranial hiatus, and it most probably originally terminated in a falciform process, which is no longer preserved on either side of this specimen.

The zygomatic process of the jugal bone is slender, and it forms a smooth arc. Compared with the same structure in most other delphinoids, however, its diameter is relatively large, and this is a primitive character state. The jugal forms a continuous connection from its point of fusion with the lachrymal bone, at the anterior margin of the orbit, spanning to the contact with a distinct facet on the anteroventral extremity of the zygomatic process of the squamosal. The postorbital process of the frontal is relatively short and broad based; it does not extend far enough ventrally to touch the anterior tip of the zygomatic process of the squamosal.

The anterior end of the left zygomatic process of the squamosal is abraded and incomplete. Its dashed outline as shown in Figure 12 is based on the complete right zygomatic process, which is inclined anteriorly, approximately rectangular in lateral view, and has a nearly flat anterior end. The postglenoid process is transversely expanded and directed ventrally. The lateral surface of the zygomatic process is rugose posteriorly in the area dorsal to the external acoustic meatus. The bony lumen of the external acoustic meatus opens in an anterolateral direction, and it lies directly posterior to the postglenoid process.

The paroccipital process is thick anteroposteriorly and curved in ventral view. The deep and narrow jugular notch separates the paroccipital process from the basioccipital crest. The right and left basioccipital crests are, for a delphinoid, relatively widely spaced, and the basioccipital bone between them is smoothly arched. Each basioccipital crest is directed ventrolaterally, and has a lobate shape, with its curved lateral edge posteromedial to the bulla. These basioccipital crests contrast with those of such primitive Odontoceti as species of Agorophiidae, in which they are more ventrally directed, not lobate, not so widely spaced, and nearly parallel to one another.

Petrosal. The right petrosal of the holotype of *A. whistleri* remains in situ within the cranium, mostly obscured by the bulla, which is also still in situ (Figs. 14 and 15). The left petrosal was removed from the cranium, and was illustrated and described by Barnes (1984a:fig.10g and 10h; 2002c:fig. 11g and 11h). In subsequent collecting at Isla Cedros, no additional petrosals having the distinctive morphology of *A. whistleri* have been discovered.

The petrosal of *A. whistleri* (Fig. 16c and 16d) measures 35 mm in overall anteroposterior length and 25 mm in maximum transverse width. It is inflated, and it is relatively large for a petrosal of a delphinoid cetacean of this body size. It is very globose and rounded in shape, with a small and rounded anterior process. Its cochlear portion is relatively large and is elongated anteroposteriorly. Its posterior process is relatively large, with a

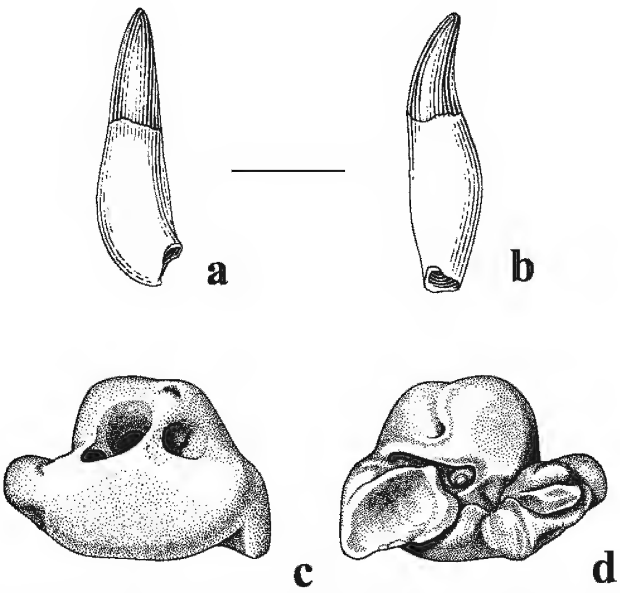

Figure 16 *Albireo whistleri* Barnes, 1984a, holotype, UCMP 314589; isolated tooth in **a**, labial view; and **b**, posterior view; left petrosal in **c**, dorsal or cerebral view; **d**, ventral or tympanic view. Scale bar (for tooth) = 10 mm, the petrosal is natural size.

concave but relatively smooth articular facet for the posterior process of the tympanic bulla.

Tympanic Bulla. The right tympanic bulla of the holotype of *A. whistleri* remains in situ within the cranium, still attached to the petrosal. The left tympanic bulla was removed from the cranium and is here for the first time illustrated (Fig.17a and 17b) and described. The bulla of *A. whistleri* is relatively large for a delphinoid cetacean, and it is moderately inflated. There is no anterior bullar process or spine (as is present in species of the Platanistidae [see Fordyce, 1994; Barnes, 2002d]), and the posterior process is relatively small. As is typical for Delphinoidea, the bulla has a lateral groove, but this groove is shallower than in most species of delphinoids. The dorsal surface of the involucrum is flat and very wide, and this is a derived character state of *A. whistleri*. The posterolateral part of the involucrum is very bulbous and extends ventrally, and this is another derived character of the species.

The referred right tympanic bulla (UCMP 324043, Fig. 17d) is virtually the same size as the holotypic bullae, which it resembles by having a very thick posterior part of the inner part of the involucrum, a deep lateral groove, and a bulbous posterior area of the outer part of the involucrum. It differs from the holotype by having a slightly wider lateral groove, especially in the posterior part.

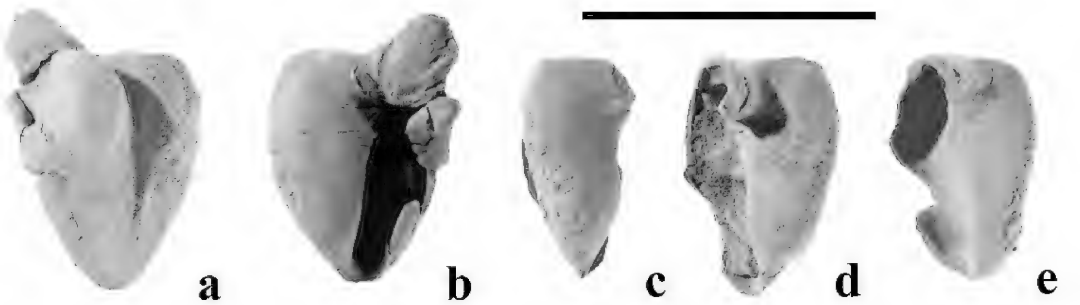

Figure 17 Tympanic bullae of *Albireo* Barnes, 1984a. **a, b**, *Albireo whistleri* Barnes, 1984a, holotypic left tympanic bulla, UCMP 314589: **a**, ventral or tympanic view; **b**, dorsal or cerebral view; **c**, *Albireo* aff. *A. whistleri* Barnes, 1984a, partial left tympanic bulla, UCMP 324044, dorsal or cerebral view; **d**, *Albireo whistleri* Barnes, 1984a, referred partial right tympanic bulla, UCMP 324043, dorsal or cerebral view; **e**, *Albireo* sp., partial right tympanic bulla, UCMP 324045, dorsal or cerebral views. Scale bar = 5 cm.

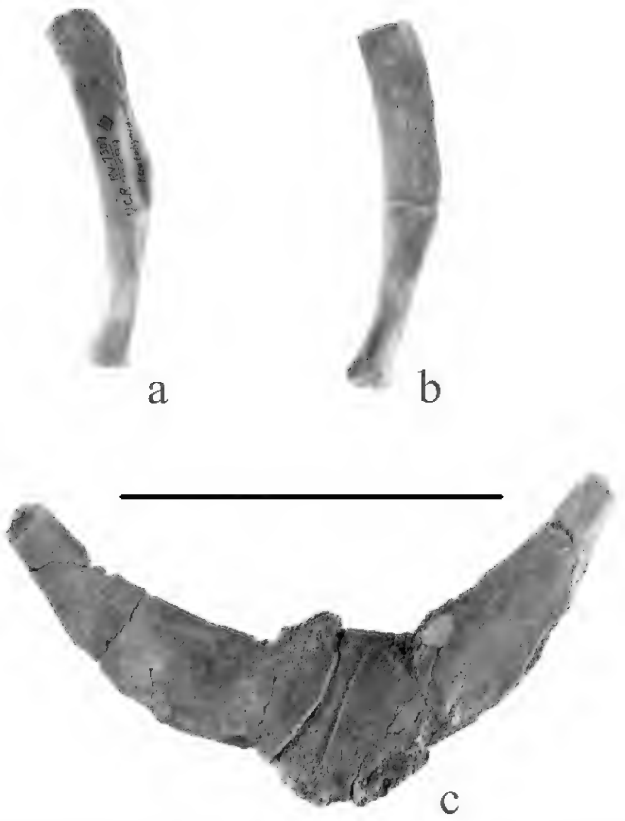

Figure 18 *Albireo whistleri* Barnes, 1984a, holotypic hyoid bones, UCMP 314589: **a**, right stylohyal in ventral view; **b**, left stylohyal in dorsal view; **c**, basihyal and fused right and left thyrohyals in dorsal view. Scale bar = 10 cm.

Hyoid Apparatus. Five bones of the hyoid apparatus are preserved with the holotype (Fig. 18). The nonpaired median element, the basihyal, is present, and it is fused with the two thyrohyals. The separate stylohyal is present, and it is fused with the epihyal. The fusion of the basihyal and thyrohyals into one unit is characteristic of all cetaceans that have attained maturity. This unit is flattened dorsoventrally, as is typical of delphinoid cetaceans, but it is very wide and is approximately twice the width of the same bone in Recent species of Delphinidae. This width is a derived character of *A. whistleri.*

Mandible. The anterior end of the left dentary is missing and has been restored with plaster. Its restored area is consistent with the length of the complete right dentary and with the estimated original length and taper of the rostrum. The measurements in Table 3 are based on the right dentary, which probably is lacking no more than 2 mm of bone from its anterior extremity.

The right and left dentaries (Fig. 19) are not firmly ankylosed, being free at the mandibular symphysis. The two horizontal rami diverge gradually posteriorly and do not diverge abruptly at the posterior end of the symphysis or at the posterior end of the tooth row, as is the case in some primitive Odontoceti and in long-snouted species. The mandibular symphysis is moderately short for an odontocete, comprising approximately 27% of the length of each dentary. Each dentary is elongate, with a dorsally curved anterior end, and this curvature is consistent with the similarly curved rostral extremity. Five or six mental foramina are located on the lateral surface of each dentary in the anterior one third of the mandible.

The angular area of the dentary descends ventrally progressing posteriorly. The angular process is broken off on both sides of the specimen, but the bone contours indicate that the angle of the dentary probably was originally prominent and that it projected posteriorly farther than does the mandibular condyle. The condyle is prominent, and it is expanded both dorsoventrally and transversely. It is buttressed by a small strut on its lateral side and is excavated on its medial side. The coronoid crest elevates posterior to the tooth row, and it has a depression in its midpart. The coronoid crest ascends to a prominent, lobate, and posteriorly directed coronoid process (Fig. 19b).

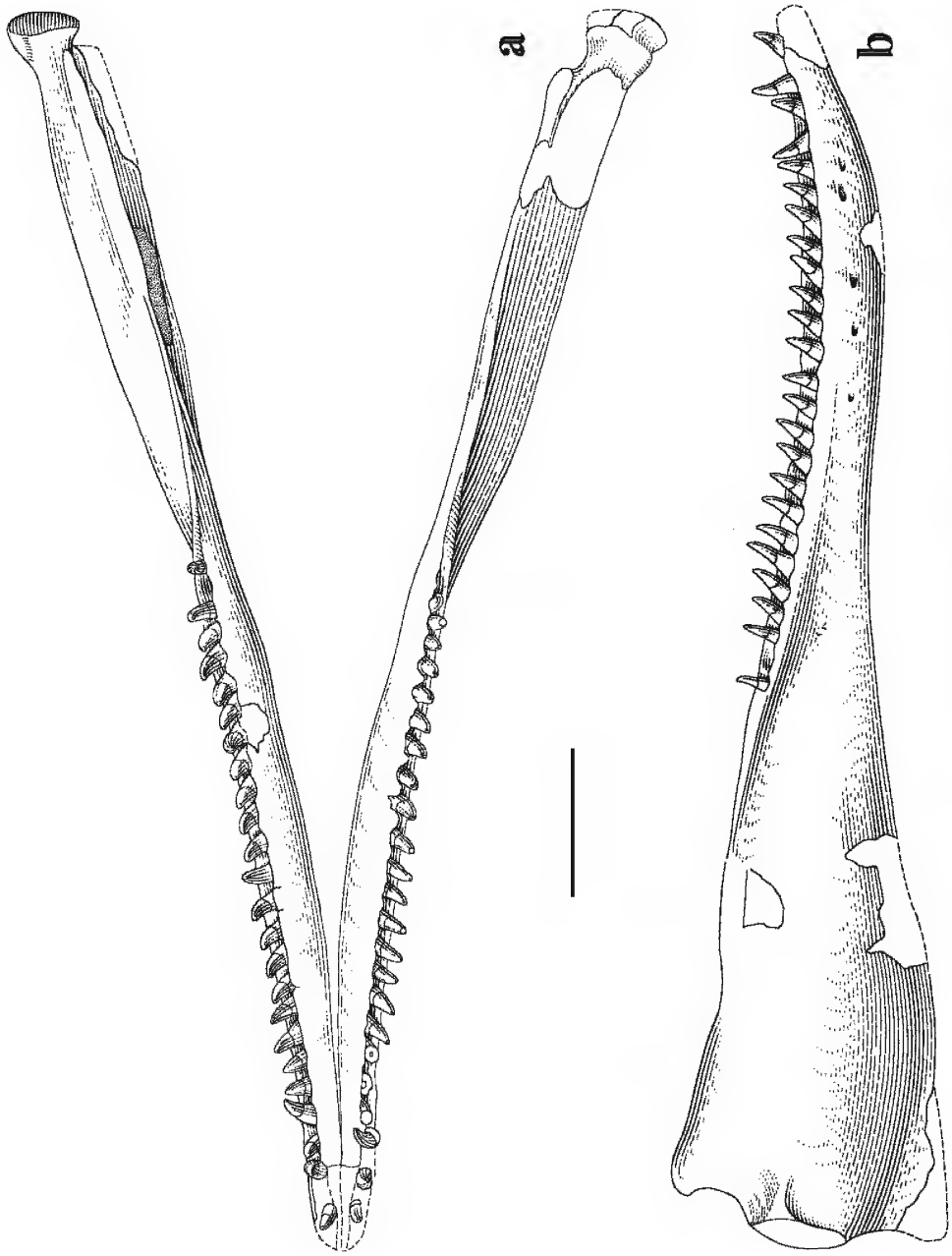

Figure 19 *Albireo whistleri* Barnes, 1984a, holotypic mandible, UCMP 314589: **a**, occlusal or dorsal view of articulated right and left dentaries; **b**, lateral view of right dentary. Scale bar = 5 cm.

The bony interalveolar septa were not fully developed. Ridges of bone mark the separations between the alveoli for the teeth, and these show that there were 25 teeth in the right dentary and an apparently equal number in the left dentary.

Dentition. The dentition of *A. whistleri* is similar to that of Recent derived species of Delphinidae by being homodont and polydont. The tooth count, apparently 25 in each side of the palate and 25 in each dentary, is greater in number than in primitive odontocetes (Barnes et al., 2002), some of which have nearly the eutherian mammalian formula, and the tooth count of *A. whistleri* is in the midrange that can be found among the later Cenozoic odontocetes.

Each tooth of *A. whistleri* has a single root and a conical crown that terminates in a sharp apical point that is curved medially toward the apex (see Fig. 16a and 16b). The tooth crowns are circular in cross section, none have cristae or carinae on their anterior or posterior sides, and the enamel is smooth, having no crenulations or wrinkles, such as are present in many primitive species of Odontoceti (e.g., species of Agorophiidae, *Xenorophus*, or Squalodontidae). Most of the teeth have crowns that are approximately 10 mm tall and 4.5 mm in diameter at the enamel line. The anteriormost teeth are not as small as they are in many Recent Delphinidae, but the posteriormost two or three teeth are approximately 30% smaller than the others.

No teeth were found in place in the rostrum. The interalveolar bony ridges in the upper tooth row are not as distinctive as they are in the dentaries, and the anterior extremity of the rostrum is broken off, thus the palatal tooth count is less definite than the mandibular tooth count. There appear to be positions for 22 maxillary teeth, and there was probably space for three premaxillary teeth on each side of the palate, as is typical of odontocetes. This would total probably 25 palatal teeth on each side, and this number equals the mandibular tooth count.

However, when the mandibular condyle of either dentary is properly articulated within its respective glenoid fossa, the dentary extends anteriorly beyond the existing anterior tip of the premaxilla and beyond the anterior tip of the rostrum as it was restored. Thus, either the rostrum was as long as the mandible, and thus contained two or three additional anterior teeth, or the rostrum was possibly slightly shorter than the mandible. Both conditions exist among living delphinid dolphins. The specimen might have some geologic distortion, however. When the mandible is correctly articulated with the cranium, the posteriormost maxillary tooth on either side does not have an opposite mandibular tooth. This might indicate that the zygomatic processes of the squamosals have been moved approximately 10 mm anteriorly relative to the braincase, and this can account for at least part of the apparent extension of the mandible beyond the approximate original rostral extremity.

The anteriormost tooth in the right dentary appears to be in place (Fig. 19b), and its procumbent orientation therefore appears to be real, as would be expected. The tooth immediately posterior to it, however, is out of position and it is oriented posteriorly. The third tooth in the right dentary has the correct inclination but is positioned more deeply in its alveolus than it would have been in life. The fourth right mandibular tooth, like the second, is also incorrectly oriented posteriorly. The 20th right mandibular tooth is missing. The other right mandibular teeth are preserved in nearly their correct original positions. In the left dentary, the fourth through sixth teeth are missing their crowns, and the last two are absent entirely.

Homodonty and polydonty in *A. whistleri* are derived characters, and both of these conditions are convergent with many other groups of derived odontocetes. The size, numbers, and spacing of the teeth and the shape of the dentary and symphysis are similar to *T. truncatus* and species of *Lagenorhynchus*. The size of the mandibular symphysis and the overall shape of the dentary are similar to those of *S. bredanensis* (Lesson, 1828).

Vertebrae. Some of the vertebrae of the holotype were articulated or were in approximately their correct anatomical sequence when the specimen was collected (Figs. 4 and 5), but several vertebrae were moved out of sequence by current action prior to final burial. The positions of the cervical vertebrae are unmistakable, and they all articulate well with one another. The thoracic vertebrae have been arranged in the probably correct anatomical sequence on the basis of the sizes of their centra, the inclination of their dorsal processes, and the positions of their transverse processes. The lumbar vertebrae have been arranged on the basis of the lengths and widths of the neural and transverse processes and the shapes of the centra. According to these lines of evidence, the vertebrae were arranged for the drawings of the reconstructed skeleton (Fig. 6) and in the photographs (Fig. 20) of the vertebral column.

The vertebral column of *A. whistleri* includes seven cervical vertebrae (as do most mammals and all Cetacea), 16 thoracic vertebrae (those vertebrae with demonstrable or likely rib attachments), and at least 24 lumbar vertebrae. No caudal vertebrae were found with the specimen, and at the locality where the specimen was discovered eroding from the sediment, the posterior part of the lumbar vertebral section had already been destroyed by erosion (Fig. 4). It is not possible to determine the original number of lumbar vertebrae or, of course, caudal vertebrae.

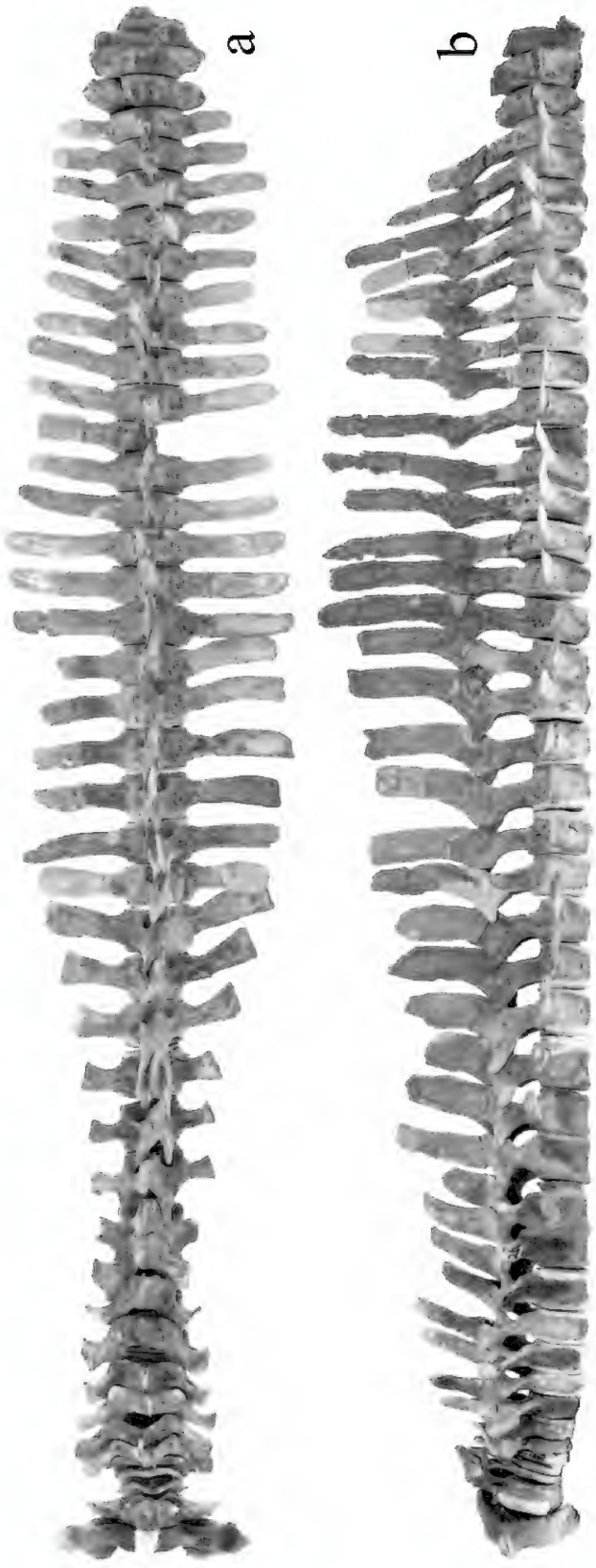

Figure 20 *Albireo whistleri* Barnes, 1984a, holotypic vertebral column as preserved, including cervical, thoracic, and anterior lumbar vertebrae, UCMP 314589; the anterior end of the vertebral column in each view is to the left side of the image: **a**, dorsal view; **b**, left lateral view.

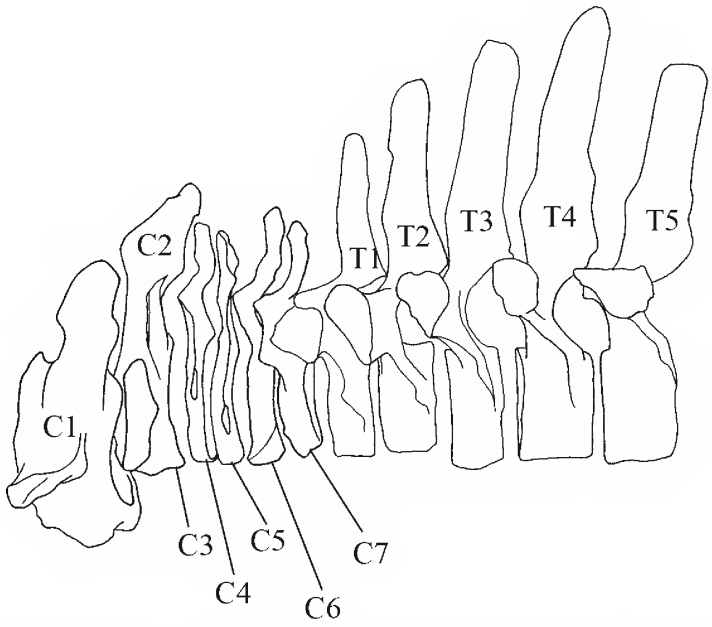

Figure 21 *Albireo whistleri* Barnes, 1984a, holotypic cervical and anterior thoracic vertebrae, UCMP 314589, in left lateral views; the cervical vertebrae are labeled C1 through C7, the first five thoracic vertebrae are labeled T1 through T5.

In general, the vertebrae of *A. whistleri* are relatively more compressed anteroposteriorly and are more numerous than they are in primitive cetaceans, and they are comparable in numbers and proportions to the vertebrae of the Recent *Lagenorhynchus albirostris* Gray, 1846 (see Slijper, 1936:fig. 204). The vertebrae are not as compressed anteroposteriorly, however, nor are they as numerous, as in the Recent species of right whale dolphins, *Lissodelphis* Gloger, 1841, nor in the living North Pacific Dall's porpoise, *P. dalli* (True, 1885), both of which have highly derived vertebral columns that contain numerous anteroposteriorly compressed vertebrae.

The series of articulated cervical vertebrae are shown in Figure 21. The atlas vertebra of *A. whistleri* (Figs. 22a, 22b, 31d) is large, flattened, and moderately compressed anteroposteriorly, is approximately oval shaped in anterior view, and has large but shallow anterior articular surfaces. A very small ventral tubercle is located beneath the very small but transversely widened fossa that received the odontoid process of the axis vertebra. On the ventral surface of the ventral tubercle is a short bony crest on each side of, and parallel to, the midline of the atlas. Each of these bony crests extends ventrally approximately 1 mm from the surface of the bone. Positioned anterolateral to each of these crests is a longer and more prominent crest that diverges posterolaterally from the midline of the vertebra; thus, these larger lateral crests flank the smaller ones that are on the ventral surface of the ventral tubercle. The atlas has on each side one relatively large, elongate, and laterally directed transverse process. The single transverse process is a derived character state in contrast to the presence of separate dorsal and ventral transverse processes in primitive Odontoceti.

The anterior articular surfaces of the atlas are broad and shallow, in accord with the wide but not prominently projecting occipital condyles of the cranium. The posterior articular surfaces are asymmetrical, both in size and shape: The right posterior articular surface has a uniform crescentic outline, but the left articular surface extends laterally onto the base of the transverse process. The intervertebral foramen, which is located dorsal to the anterior articular surface, is incompletely formed. It is represented by a transverse sulcus bordering the dorsal margin of the articular surface, but unlike the condition in generalized mammals and primitive Cetacea, the dorsal part of this foramen is atrophied.

The anteroposterior compression of the atlas vertebra of *A. whistleri* is consistent with the evolutionary trend of progressive anteroposterior shortening of the cervical vertebrae in various delphinoid lineages. Its relatively long transverse processes might be considered to be a primitive character state because the transverse processes are elongate in the Archaeoceti (see Kellogg, 1936). However, in the case of *A. whistleri*, it is most likely that the transverse processes have

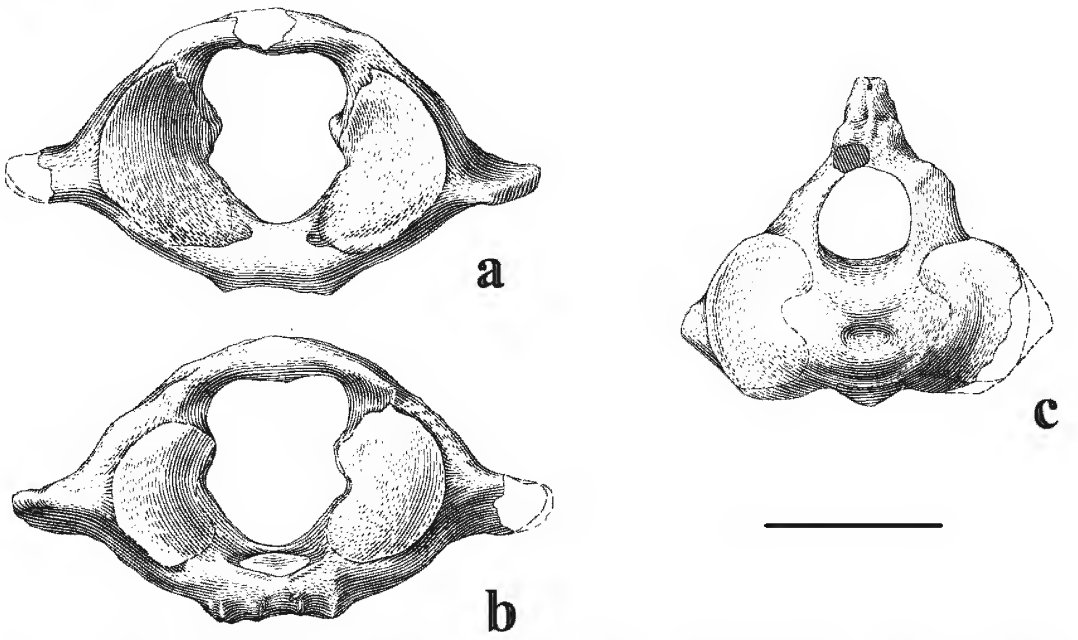

Figure 22 *Albireo whistleri* Barnes, 1984a, holotypic cervical vertebrae, UCMP 314589: **a**, anterior view of atlas vertebra; **b**, posterior view of atlas vertebra; **c**, anterior view of axis vertebra. Scale bar = 5 cm.

become secondarily re-elongated because they are approximately of the same proportion as they are on the atlas vertebra of *Kentriodon pernix* (see Kellogg, 1927:pl. 12, figs. 3 and 4). It is logical to assume that Middle Miocene *K. pernix* represents a more generalized delphinoid morphology than the geochronologically younger and morphologically more derived Albireonidae. The transverse processes project horizontally from the body of the vertebra, and this is a derived character state compared with the situation in *K. pernix*, in which the transverse processes of the atlas vertebra are oriented ventrolaterally.

Compared with the atlas vertebra of *A. savagei*, sp. nov., the atlas of *A. whistleri* differs by being absolutely and relatively narrower and by having a lower neural arch. Its transverse process does not project so far laterally, but it is larger and more expanded in an anteroposterior plane. The atlas of *A. whistleri* is thicker anteroposteriorly, both measurably and proportionally, than that of *A. savagei* (see Table 4).

The axis vertebra of the holotype of *A. whistleri* (Figs. 21 [where it is labeled as C2], 22c, 23a) is missing the left transverse process, but is otherwise complete. It is a very odd axis vertebra compared with axes of other delphinoids: The odontoid process is greatly reduced, represented only by a small tuberosity; the centrum of this vertebra is very deep dorsoventrally; the transverse processes have large and wide anterior articular facets; the extremity of the transverse process is reduced to being only a small, triangular projection; and the neural canal is a vertically oriented oval. The neural process is thick anteroposteriorly, and it slopes posterodorsally. Extrapolating from its half-width, when complete, the axis was approximately 100 mm in transverse width. Its fully preserved vertical dimension is 93 mm.

The third through seventh cervical vertebrae are greatly atrophied bones when compared with the atlas and axis (Fig. 21). The centrum and the neural arch of the third cervical vertebra are both very thin anteroposteriorly. The centrum measures only 1–2 mm thick, and the uncertainty about its thickness is because the entire centrum is firmly fused to the posterior side of the axis. These two are the only vertebrae in the holotypic skeleton that are fused. The third cervical vertebra had very reduced transverse processes, being triangular in shape and projecting only 5 mm beyond the lateral margin of the posterior vertebral epiphysis. It has a complete neural process, which has a well-formed dorsal spine that is firmly appressed to, and apparently fused to, the posterior side of the neural spine of the axis (see Fig. 21).

Cervical vertebra 4 (Fig. 23b) is very flattened anteroposteriorly, and its centrum, which is only partly preserved, is irregular in its thickness, which varies from approximately 6 to 8 mm. The dorsal transverse process is preserved only on the left side, and it is a small triangular projection. The ventral part of the vertebra is broken, and there is no way to determine whether a ventral

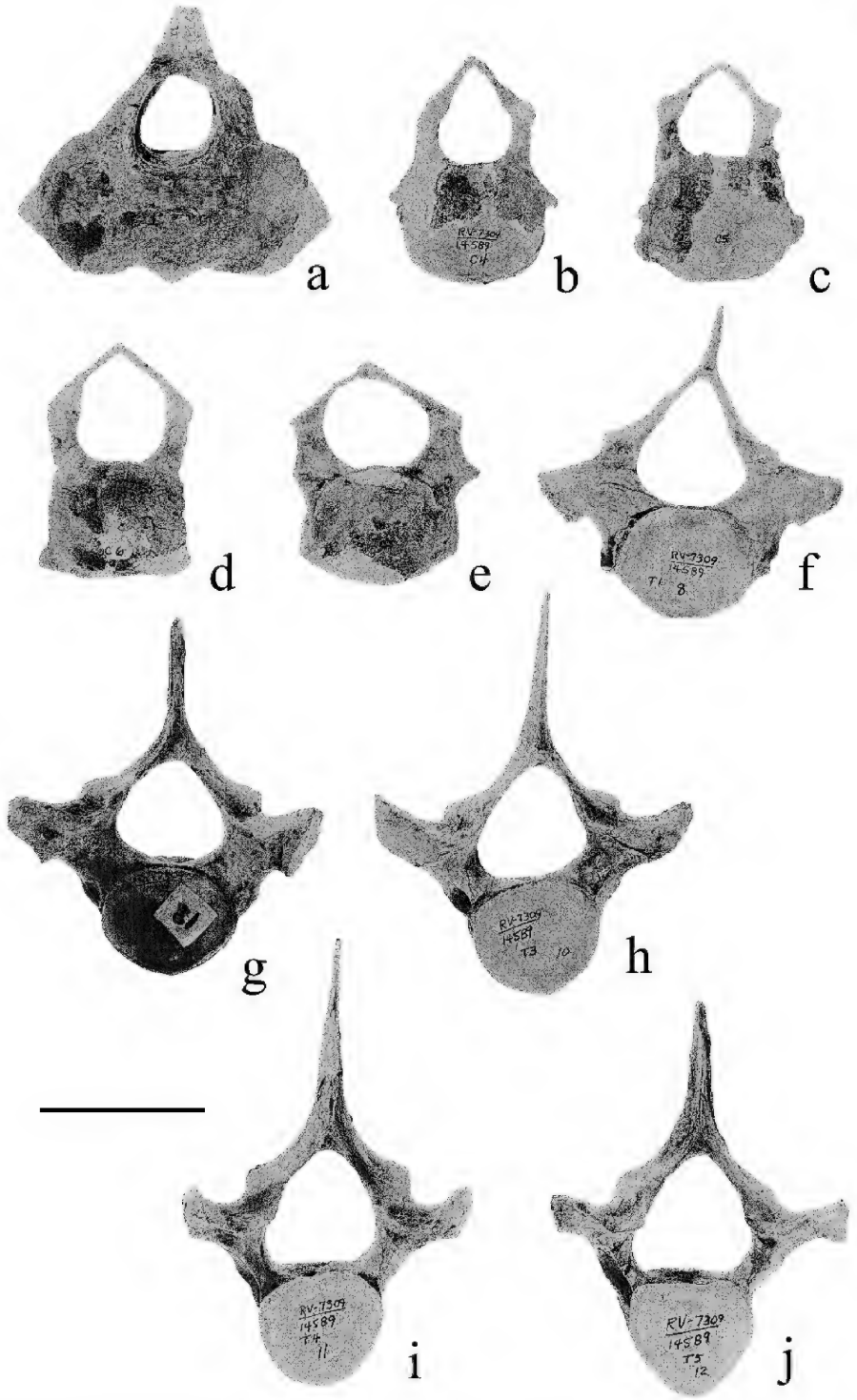

Figure 23 *Albireo whistleri* Barnes, 1984a, anterior views of holotypic vertebrae, UCMP 314589: **a**, axis or second cervical vertebra, which has the third cervical vertebra fused to its posterior surface; **b**, fourth cervical vertebra; **c**, fifth cervical vertebra; **d**, sixth cervical vertebra; **e**, seventh cervical vertebra; **f**, first thoracic vertebra; **g**, second thoracic vertebra; **h**, third thoracic vertebra; **i**, fourth thoracic vertebra; **j**, fifth thoracic vertebra. Scale bar = 5 cm.

transverse process previously existed. The pedicle of the neural arch is extremely delicate, and the prezygapophysis is very small.

Cervical vertebra 5 (Fig. 23c) is likewise very flattened anteroposteriorly, and its centrum, which is partly preserved, is irregular in thickness, varying from approximately 6 to 7.5 mm. On the right side of this vertebra, both the dorsal and ventral transverse processes are preserved, and each of these processes has the shape of a small triangular projection. They clearly terminate laterally, not joining laterally to enclose a transverse foramen, as is typically the situation in primitive Odontoceti and in most cetaceans. The pedicles of the neural arch are very delicate, and there is a very small prezygapophysis preserved on the right side.

Cervical vertebra 6 (Fig. 23d) is also flattened anteroposteriorly, and its centrum is irregular in thickness, varying from 7 to 8 mm. The centrum of this vertebra is wider and more square in anterior or posterior view than are those of cervical vertebrae 3 through 5. Its ventral transverse process is fully preserved on the right side, and although this process is larger than its homologue on cervical vertebra 5, it is likewise shaped as only a small triangular projection, which on this vertebra projects posterolaterally rather than laterally. The dorsal transverse process is preserved on the left side of the sixth cervical vertebra, and it is represented merely by some tiny, triangular tubercles that project laterally from the vertebra. On the basis of these two transverse processes, which are on opposite sides of the vertebra, each process clearly terminates laterally. The two processes were not originally joined laterally to enclose a transverse foramen, as is the case in primitive Cetacea. The pedicle of the neural arch is very delicate, and the base of a very small prezygapophysis is preserved on each side.

Cervical vertebra 7 (Fig. 23e) is the largest of the cervical vertebrae posterior to the axis. It is flattened anteroposteriorly, and the anteroposterior thickness of its centrum varies from 7 to 10 mm. The centrum of cervical vertebra 7 is wider and more nearly rectangular in face view when compared with those of cervical vertebrae 3 through 6. Its dorsal transverse process is a laterally projecting triangular point that, rather than originating from the lateral side of the centrum, originates from the lateral side of the pedicle. On the left side of the vertebra, the ventral transverse process is preserved, and it is only a small protuberance at the ventrolateral corner of the centrum. The dorsal and ventral transverse processes are thus widely separated and they clearly did not join laterally to enclose a transverse foramen as exists in primitive Cetacea. The pedicle of the neural arch is very delicate, but it is wider transversely than are the pedicles of cervical vertebrae 3 through 6. The prezygapophyses of this vertebra, while small, are larger than those on cervical vertebrae 3 through 6, and they are fully formed on each side of the specimen.

The centra of the thoracic vertebrae are relatively compressed anteroposteriorly. Thoracic vertebra 1 (Fig. 23f) has a centrum that is wider than it is tall, is anteroposteriorly compressed, and has narrow pedicles and neural arch and a short and delicate neural process. In contrast, thoracic vertebra 14 has a more barrel-shaped centrum, is not so much anteroposteriorly compressed, and has anteroposteriorly expanded and flattened pedicles and very long neural and transverse processes.

From the anterior thoracic vertebrae to the posterior lumbar vertebrae of *A. whistleri*, the centra become progressively narrower and ventrally more strongly keeled in the mid part of the thorax, the transverse processes become progressively longer and more flattened dorsoventrally and positioned more ventrally on the vertebral centrum rather than on the lateral side of the pedicle. Thoracic vertebrae 1 through 9 retain articulations with both the capitula and tubercula of their ribs. From thoracic vertebra 10 through 16, the capitulum of each rib has lost its contact with the vertebra, and only the tuberculum of the rib makes contact at the extremity of the lengthened transverse process.

All of the lumbar vertebrae have anteroposteriorly shortened centra that are nearly circular in anterior and posterior views (Figs. 24 and 25). They have very elongate and comparatively narrow transverse processes and neural processes. The transverse processes are directed laterally and are positioned at midheight on the centrum, and this is the derived character state that is typical of virtually all modern Cetacea. In contrast, among the Archaeoceti (see Kellogg, 1936:pls. 4-6; Uhen, 2004:figs. 81, 83, 85, 87) and primitive Mysticeti (see Emlong, 1966:fig.12), the transverse processes are directed ventrolaterally, as they are in many generalized, large-bodied, terrestrial mammals. The elongate and slender transverse and neural processes on the posterior thoracic vertebrae and lumbar vertebrae of *A. whistleri* are a derived character state and contrast with the shorter and broader processes on the same vertebrae of Kentriodontidae such as *Kentriodon* (see Kellogg, 1927) and *Atocetus nasalis* Barnes, 1985c (see Barnes, 1985c, 1988b).

In *A. whistleri*, the prezygapophyses of all of the dorsal vertebrae are reduced in size, and they have the shape of a transversely compressed, anteriorly projecting tab. The prezygapophyses of the posterior thoracic and of the lumbar vertebrae have lost their articular facets because the vertebrae in this part of the body entirely lack postzygapophyses. The prezygapophyses decrease

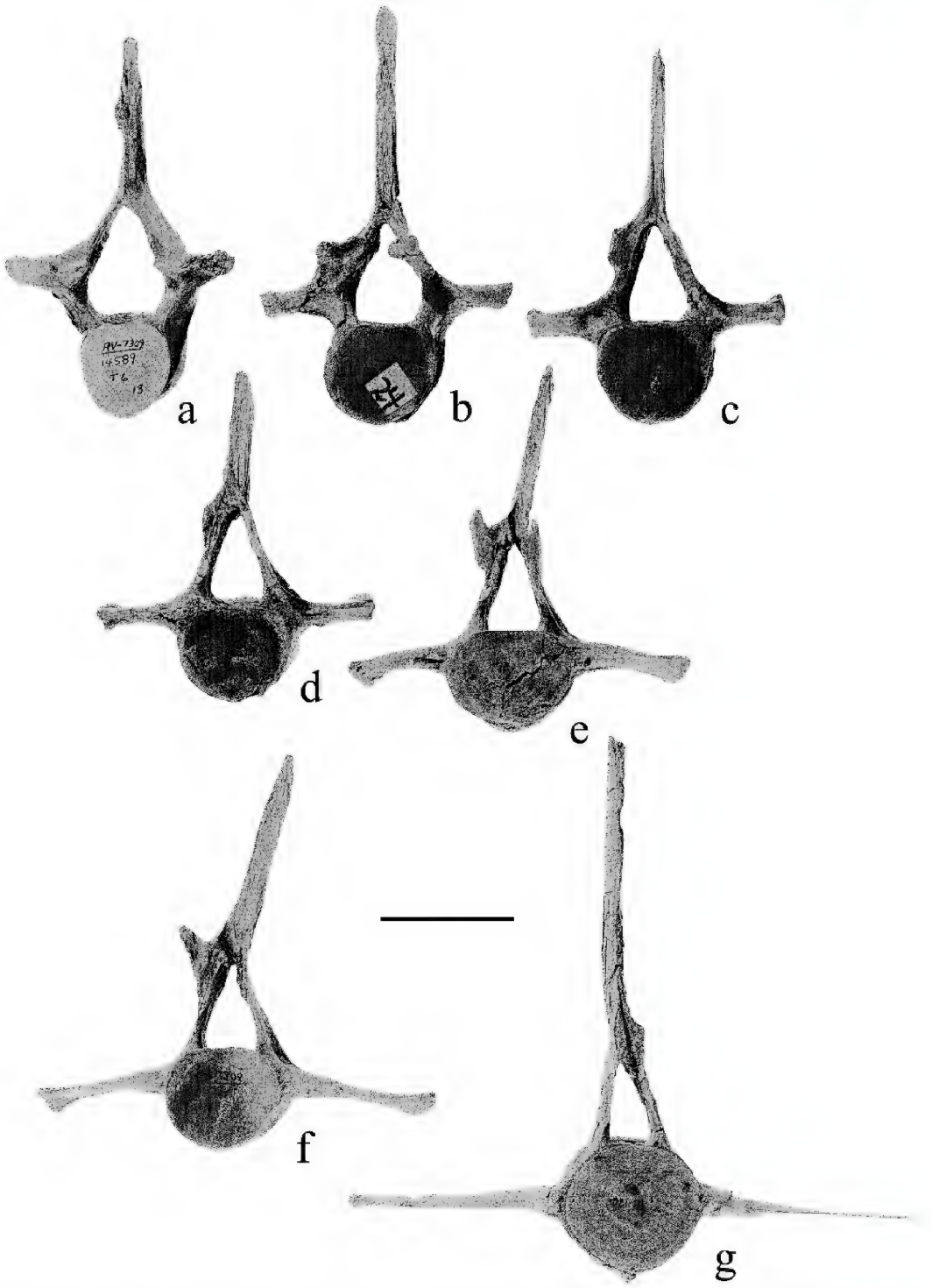

Figure 24 *Albireo whistleri* Barnes, 1984a, anterior views of holotypic thoracic vertebrae, UCMP 314589: **a**, sixth thoracic vertebra; **b**, seventh thoracic vertebra; **c**, eighth thoracic vertebra; **d**, ninth thoracic vertebra; **e**, 10th thoracic vertebra; **f**, 11th thoracic vertebra; **g**, 12th thoracic vertebra. Scale bar = 5 cm.

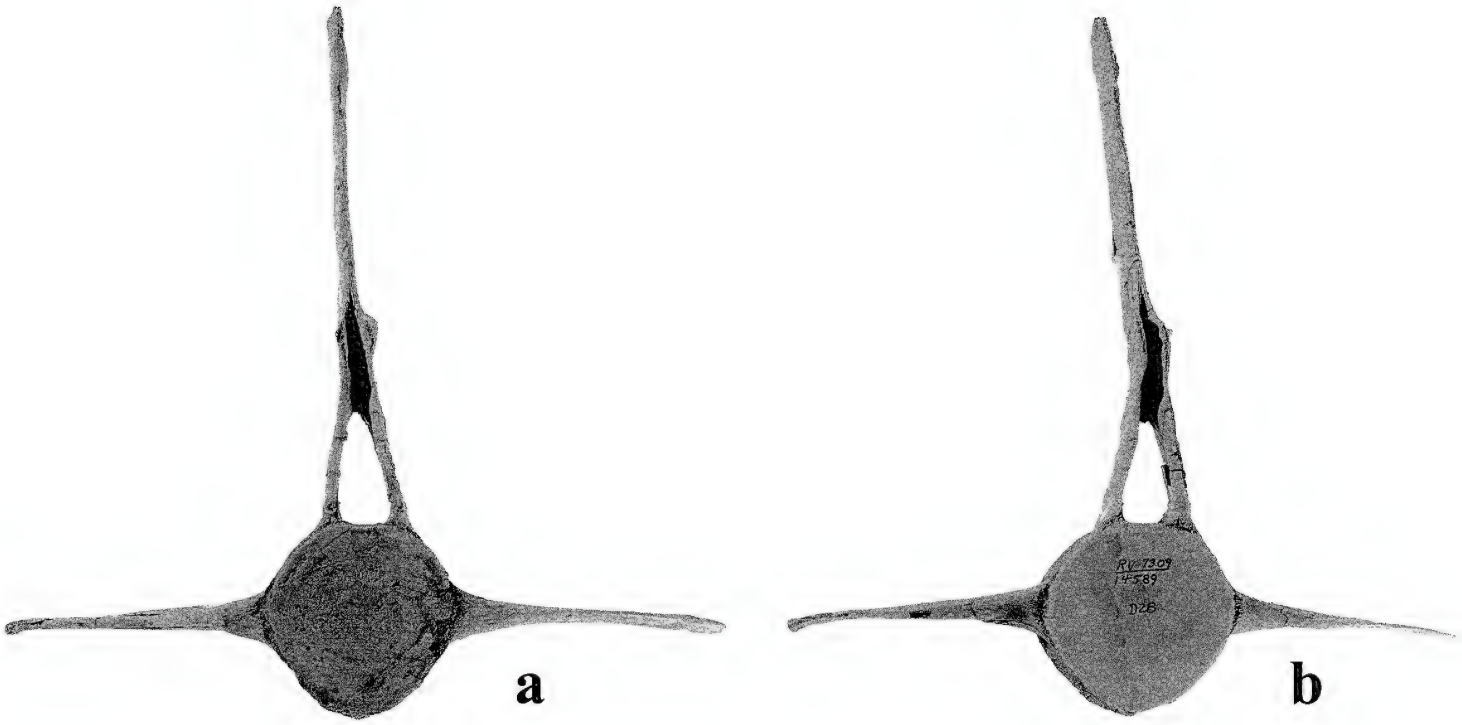

Figure 25 *Albireo whistleri* Barnes, 1984a, anterior views of holotypic lumbar vertebrae, UCMP 314589: **a**, first lumbar vertebra; **b**, second lumbar vertebra. Scale bar = 5 cm.

in size progressing posteriorly through the sequence of thoracic and the lumbar vertebrae. All of these are derived character states, and this same phenomenon has also developed convergently among various clades of Cetacea.

Ribs. On the basis of the presence of partial ribs on both sides of the preserved skeleton and on the numbers of vertebrae that have rib attachments, it can be determined that there were 16 ribs on each side of the thorax of *A. whistleri* (Fig. 26). The first rib of *A. whistleri* is unusually short and very wide transversely compared with the same rib in living species of Delphinidae, and this is a derived character state. Proceeding posteriorly, the ribs become progressively more slender. The more anterior ribs curve anteriorly near their distal ends, whereas the ends of the more posterior ribs are directed posteriorly (Fig. 6). The first nine ribs have both capitula and tubercula, but the posterior seven ribs have only the tuberculum, and the tuberculum of each rib was in life attached at the distal end of the transverse process of the respective vertebra. The lack of a capitulum on the posterior ribs is typical of Cetacea, but the number of such ribs is variable among different species (see Slijper, 1936:380–386; Winge, 1942:248). The posterior six ribs of *A. whistleri* abruptly decrease in both size and length compared with the more anterior ribs.

Sternum and Sternal Ribs. The manubrium is the only ossified sternebra that was found with the holotypic skeleton. It is flattened dorsoventrally and has a facet for a sternal rib attachment at each corner. Ribs 1 and 2 appear to have been the only ones that in life were articulated, via ossified sternal ribs, with the manubrium. Ribs 3 through at least 9 also were attached distally to well-formed ossified sternal ribs (Fig. 27), and these sternal ribs in life certainly would have had cartilaginous extensions to cartilaginous sternebrae. The ossified sternal ribs are all approximately the same size, rodlike in their shapes, and slightly expanded at both their proximal and distal ends. Ribs 10–16 appear not to have been attached in life to any ossified sternal ribs (Fig. 6).

Forelimb. Many bones of both of the forelimbs are preserved with the holotypic skeleton. The scapula is relatively large for the body size of the animal, but it is not very wide, and its blade is very thin and delicate. The humerus, radius, and ulna are by comparison relatively short.

Neither scapula of the holotype is complete, but all of the features of this bone are preserved on either one scapula or the other. Of the two, the right scapula (Fig. 28b) has the more complete vertebral border and coracoid process, and the left scapula (Fig. 28a) has the more complete acromion process and glenoid fossa, and it has the best preserved overall shape. The right scapula has been broken, and its proximal and distal parts have been reunited incorrectly so that its glenoid fossa and acromion and coracoid processes are artificially tilted too much in an anterodistal direction. This part of the left scapula is anatomically correct (Fig. 28a).

The scapula of *A. whistleri* (Figs. 28a, 28b, 29, 30) is, for a delphinoid, relatively tall and narrow and is not shaped as a semicircular fan, a shape that is typical of many Cetacea. The vertebral border of the scapula forms a smooth arc. The supraspinatus fossa is very small, and the infraspinatus fossa thus occupies most of the area of the lateral surface of the blade of the scapula. Two low ridges emanate from distal part of the scapula, each radiating toward the vertebral border. The acromion process, which is entirely preserved on the left scapula, curves in an anteromedial direction. It is greatly expanded distally, so much so that the distal width of the process is more than twice the width at its base. The coracoid process is elongate and flattened, has nearly parallel margins, and is slightly expanded at its anterior extremity. On the right scapula, the slight curvature of this process is well preserved. The glenoid fossa is oval shaped and is expanded slightly in an anteroposterior direction. The right scapula measures a maximum of 192 mm across its undistorted vertebral border. The undistorted left scapula measures 161 mm in maximum height from the borders of its glenoid fossa to the vertebral border. In its overall shape, the scapula is shaped much like those of the distantly related Recent Amazon dolphin (*Inia geoffrensis* (Blainville, 1817)) and bottlenose dolphin (*T. truncatus*).

The humerus of *A. whistleri* (Figs. 28c, 28d, 29, 30) is relatively short and anteroposteriorly expanded for a delphinoid, and it has a thick shaft. The humeral head is proportionally large, and instead of the typical hemisperical shape as is present in most Cetacea, it is ovoid, and it is directed laterally. The greater and lesser tuberosities are merged into an anteroposteriorly wide and blocky eminence that projects farther proximally than does the head of the humerus. The anterior border of the humerus is formed into a narrow edge that lacks any sort of definite deltoid tuberosity, and this is an apomorphy of *A. whistleri*. Distally, the anterior edge of the humerus expands anteriorly immediately proximal to the radial facet. The posterior border of the diaphysis of the humerus expands posteriorly immediately proximal to the ulnar facet. The ulnar facet is nearly the same size as the radial facet, and this is different from the situation in most Cetacea, in which the ulnar facet is typically much smaller than the radial facet. Also differing from most cetaceans, the ulnar facet is not clearly divided into two planes; it forms only one plane, and it does not curve far proximally onto the posterior side of the shaft of the bone. The posterior side of the humerus is extended

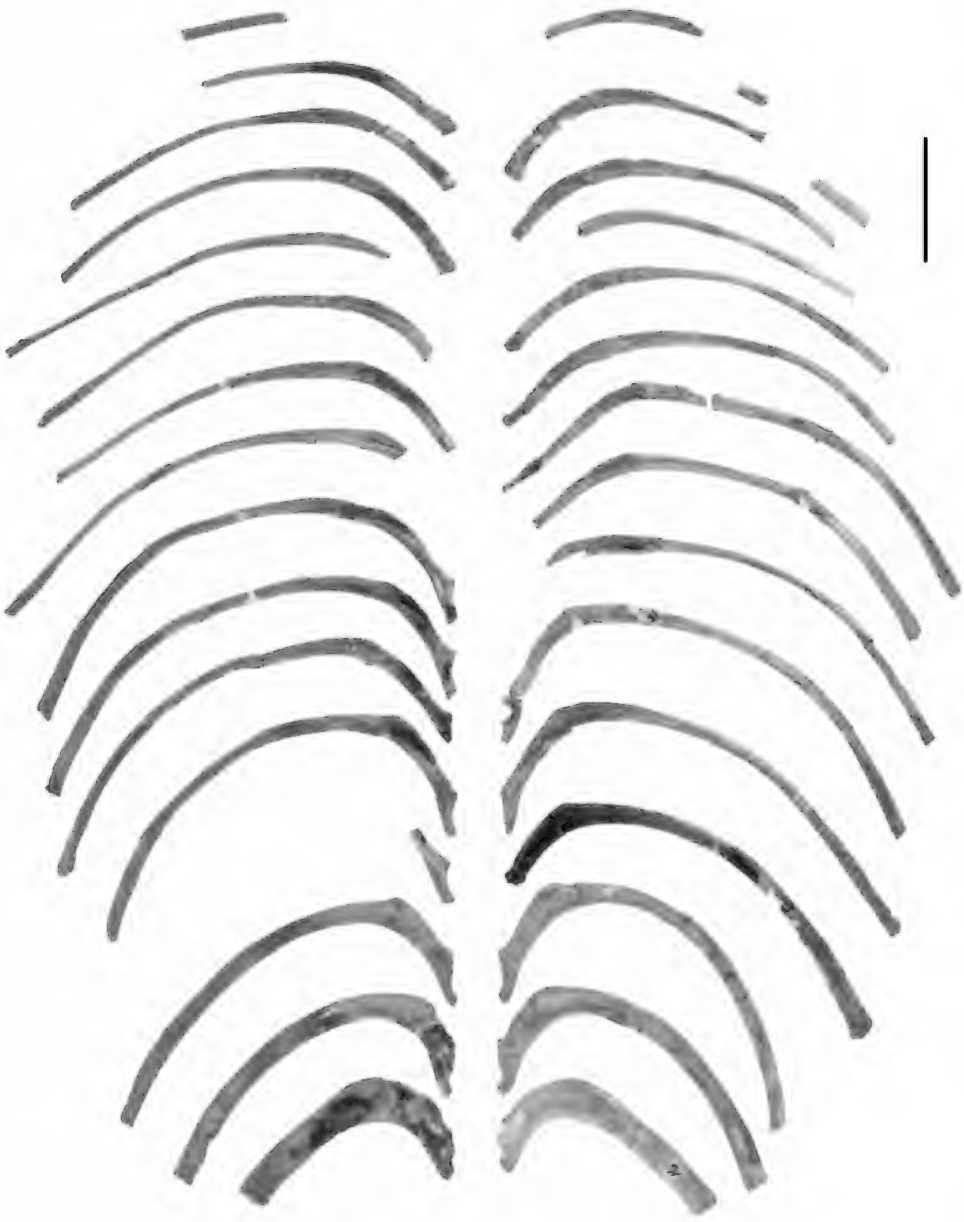

Figure 26 *Albireo whistleri* Barnes, 1984a, holotypic right and left ribs, UCMP 314589, in anterior views; arranged in probable anatomical sequence, right ribs are in the top part of the image, left ribs in the lower part, anterior is to the left side of the image. Scale bar = 10 cm.

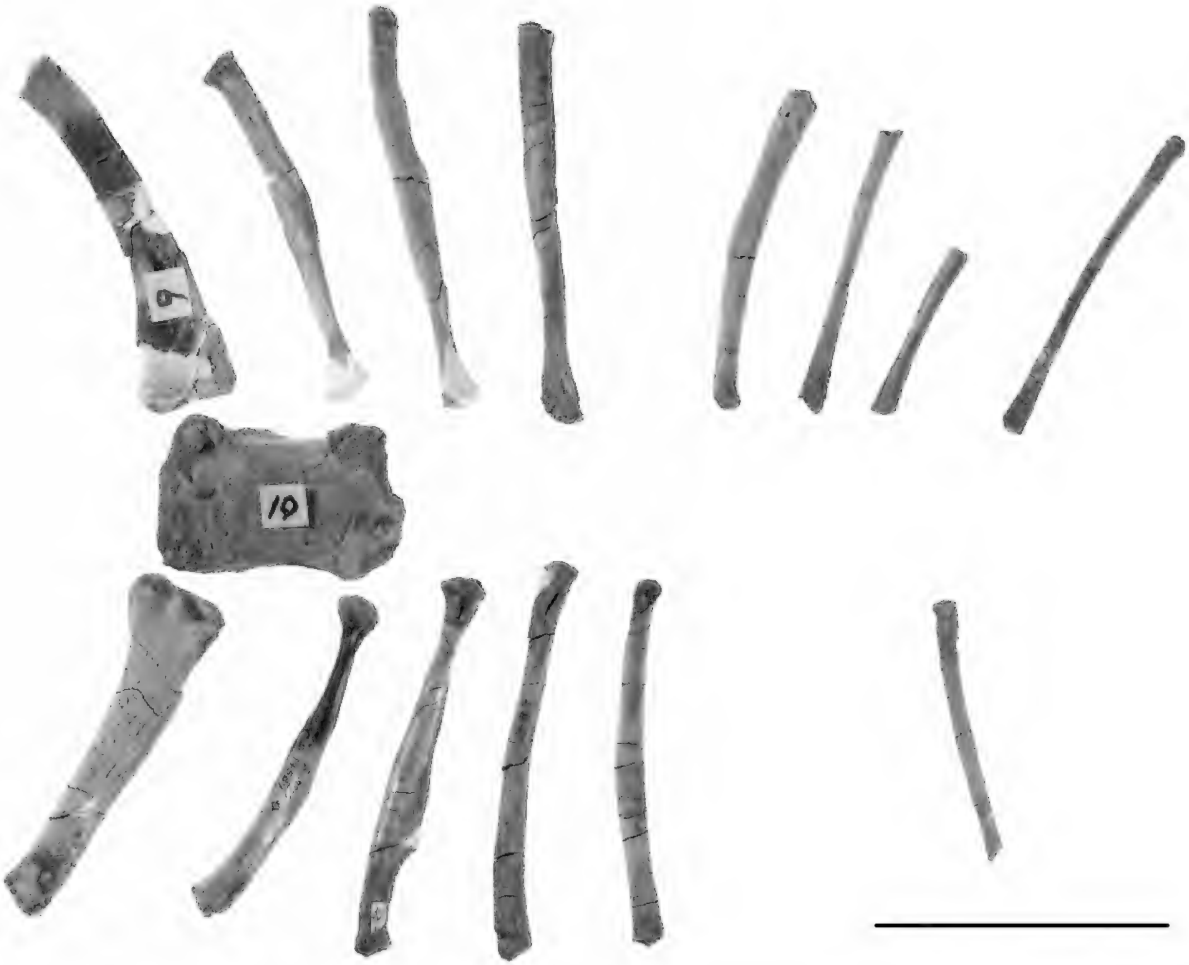

Figure 27 *Albireo whistleri* Barnes, 1984a, holotypic manubrium and right and left ossified sternal ribs, UCMP 314589, in dorsal view; arranged in probable anatomical sequence, right sternal ribs are in the top part of the image, left sternal ribs in the lower part, anterior is to the left side of the image. Scale bar = 10 cm.

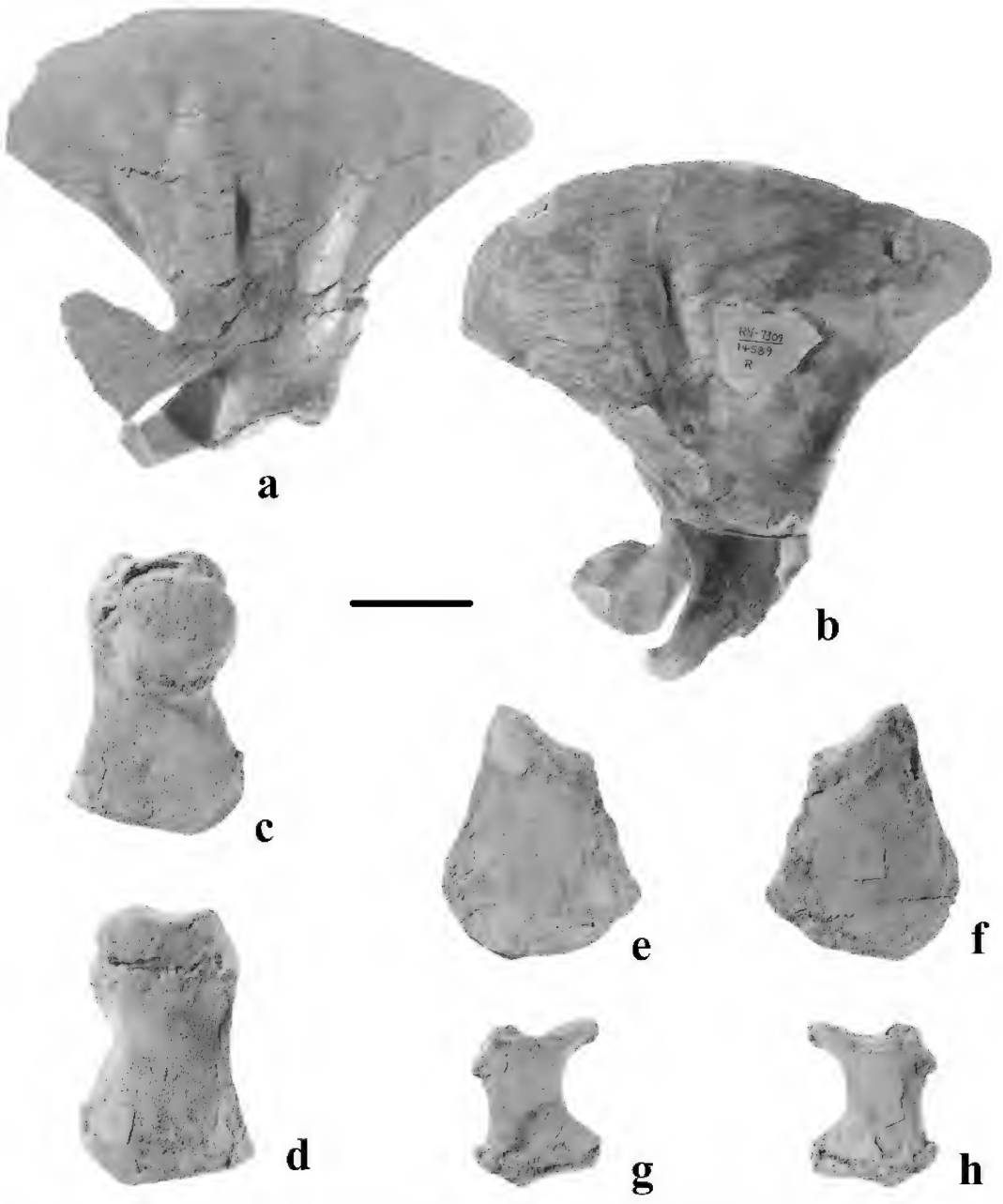

Figure 28 *Albireo whistleri* Barnes, 1984a, holotypic forelimb elements, UCMP 314589: **a**, lateral view of left scapula; **b**, medial view of right scapula; **c**, lateral view of left humerus; **d**, medial view of left humerus; **e**, lateral view of left radius; **f**, medial view of left radius; **g**, lateral view of left ulna; **h**, medial view of left ulna. Scale bar = 5 cm.

posteriorly where the olecranon process of the ulna would articulate. The more complete left humerus measures 97 mm in maximum length, and the right humerus measures 70 mm in maximum anteroposterior width across its distal end.

The left radius of the holotype (Figs. 28e, 28f, 29, 30) is virtually complete, whereas the right radius was broken and is distorted. The radius of *A. whistleri* is relatively short for the body size of the animal. The left radius measures 93 mm in maximum length, and it is very much expanded distally, almost fanlike, measuring 72 mm in maximum width in the anteroposterior plane. Of all known cetaceans, the radius of *A. whistleri* is the most expanded of any in the anteroposte-

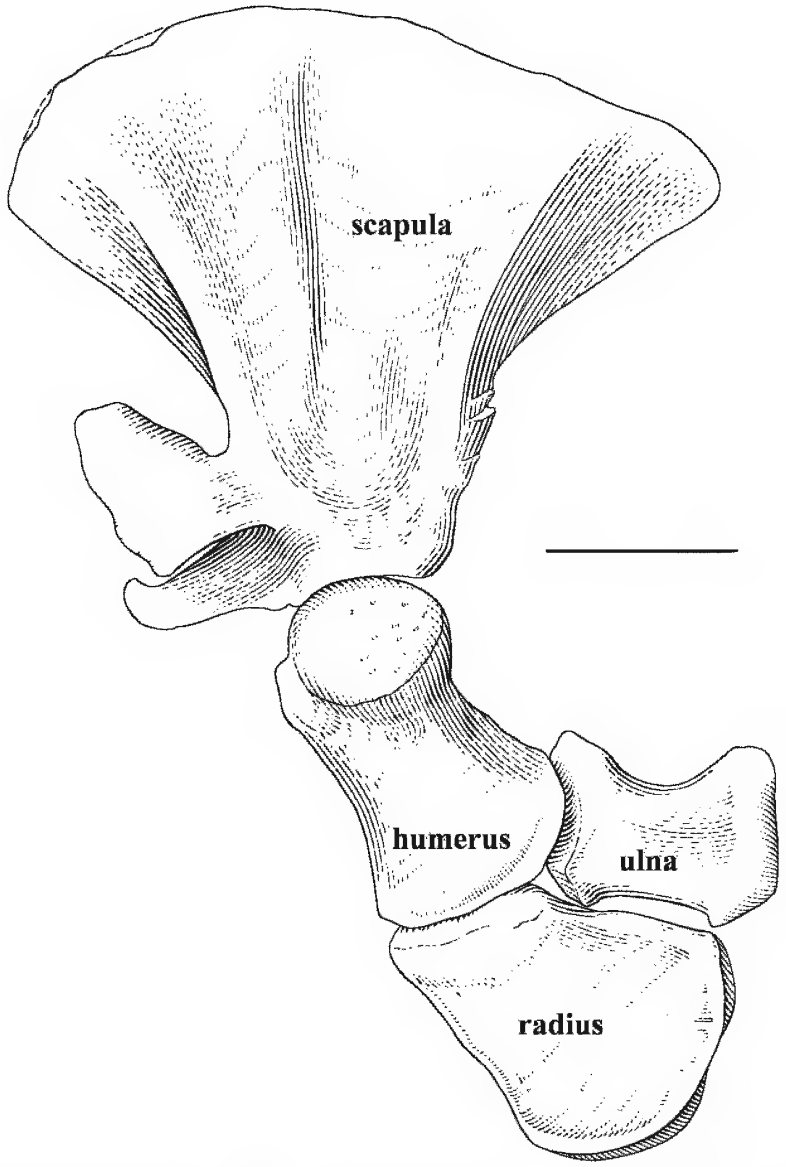

Figure 29 *Albireo whistleri* Barnes, 1984a, holotypic left forelimb bones in lateral view, UCMP 314589, showing the articulation of the scapula, humerus, radius, and ulna. Scale bar = 5 cm.

rior plane. The shortness and width of the pectoral flipper and the humerus and radius are emphasized in that these two bones have almost equal lengths, and each of them has its maximum anteroposterior width at the distal end.

The ulnae of the holotype are of different lengths, and this difference is probably caused by geologic distortion of the distal part of the right ulna. The shorter left ulna (Figs. 28g, 28h, 29, 30) appears to represent the true length of this bone, which is extremely short, and has a functional length, measured at the middle of the proximal articular surface, of only 55 mm. The right ulna has the more completely preserved proximal end. The distal end of the ulna is extremely expanded in an anteroposterior plane measuring 47 mm on each bone, neither of which is complete; thus, either ulna of this specimen in life would have measured approximately 2 or 3 mm more than 47 mm. The olecranon process is not large, nor is it curved or directed proximally, as is typical of most Cetacea and certainly of other delphinoids. Instead, the olecranon process of the ulna is narrow, and it extends posteriorly and is long,

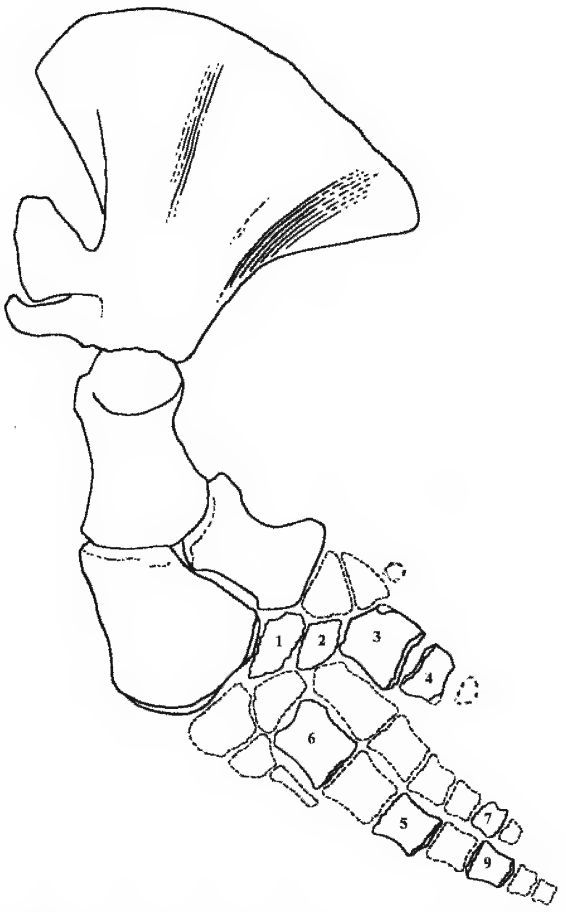

Figure 30 *Albireo whistleri* Barnes, 1984a, holotypic left forelimb in lateral view, UCMP 314589, partially reconstructed, showing possible positions of nine preserved metacarpal and carpal bones, labeled 1 through 9 reflecting the laboratory labels that are affixed to the specimen, with missing bones added, indicated by dashed lines, based on the morphology of the forelimb of the Recent bottlenose dolphin, *Tursiops truncatus*, and the common dolphin, *Delphinus delphis*.

extending posteriorly approximately 20 mm from the diaphysis of the ulna. The shortness and expansion of the diaphysis and the modifications of the olecranon process are all autapomorphies of *A. whistleri*.

The anteroposterior expansion of the radius and ulna of *A. whistleri* and the loss of the olecranon process of the ulna are similar to the conditions in the living platanistid, the Ganges River Dolphin (*Platanista gangetica* [Lebeck, 1801]), and in the living iniid, the Amazon Dolphin (*I. geoffrensis*). These modifications certainly developed convergently in these different species.

The holotypic specimen includes two metacarpals: one larger and one smaller. They were found in the sediment close to the left forelimb bones, and possibly they are from the left pectoral flipper. Each of these metacarpals is approximately a four-sided parallelogram. Each measures 13 mm in transverse (plantar/palmar) thickness. If it can be assumed that in life approximately 3 mm of flesh covered each side of the pectoral flipper, as is typical of medium-sized living delphinoids, it can be estimated that in life the pectoral flipper of *A. whistleri* was approximately 19–20 mm thick, in the plantar/palmar dimension. Because of the variability in the sizes and shapes of the metacarpals of living Cetacea, it is not possible to accurately identify which position each of these metacarpals occupied in the pectoral flipper of the holotype. The two bones are represented in the reconstructions of the holotypic skeleton (Figs. 6a and 30) as generalized metacarpal bones.

The holotype of *A. whistleri* includes nine phalanges, both large and small. Each phalanx is flattened transversely, wide anterposteriorly, and flat both apically and distally. Because of the variability in the sizes and shapes of the phalanges

in cetaceans, and the fact that these bones were not found articulated, it is not possible to accurately identify which position each of these bones occupied, or even to which flipper they belonged. These phalanges are represented in the reconstruction (Fig. 30) in an arrangement that is possible, but which is not demonstrably correct. In the skeletal and forelimb restorations, the missing bones and the phalangeal formula are based on Recent *Tursiops truncatus* and *Delphinus delphis*.

Albireo aff. *A. whistleri* Barnes, 1984a
Figure 17c

SPECIMEN. UCMP 324044, incomplete left tympanic bulla, collected by Frank H. Kilmer, 28 February 1964, field number FK 33a.

LOCALITY. UCR locality RV-7340, at Kilmer's Discovery Locality, found loose on the surface of Unit 12 (= Unit L) of the Lower Member of the Almejas Formation, approximately 30 to 50 feet (~9–15 m) stratigraphically above the level of the holotype of *A. whistleri*, in south-facing badlands on the southeast corner of Isla Cedros, Baja California, Mexico.

DESCRIPTION. This partial left tympanic bulla is slightly smaller than the holotypic bulla of *A. whistleri*, which it resembles by having the anterior part of the medial part of its involucrum very thick, both transversely and dorsoventrally, and by having a prominent and dorsoventrally deep posterior part of the involucrum. It differs from both the holotype and the referred (UCMP 324043) tympanic bullae of *A. whistleri* by being slightly smaller.

DISCUSSION. Because this specimen was recovered from a higher stratigraphic position than the holotype and referred specimen of *A. whistleri* (see Fig. 2) and because of its smaller size, I have identified it less precisely and believe that it might be a more derived taxon, but one that is closely related to *A. whistleri*.

Albireo sp.
Figure 17e

SPECIMEN. UCMP 324045, incomplete right tympanic bulla, collected by Richard H. Tedford and David P. Whistler, 9 August 1965, field number RHT 1304.

LOCALITY. UCR locality RV-7307, Richard H. Tedford Field Locality 2, from Unit 12 (= Unit L) of the Lower Member of the Almejas Formation, approximately 60 to 70 feet (~18–21 m) stratigraphically above the base of the Almejas Formation, in south-facing badlands near the southeast corner of Isla Cedros, Baja California, Mexico. This is the same locality and the same stratigraphic horizon that yielded the holotypic partial skeleton (UCMP 315975, formerly UCR 15975) of the phocoenid porpoise *Piscolithax boreios* Barnes, 1984a (see Barnes, 1984a:25, fig. 8), and a referred partial skeleton (UCMP 315258, formerly UCR 15258) of an adult male of the otariine pinniped *Thalassoleon mexicanus* Repenning and Tedford, 1977. This isolated tympanic bulla of *Albireo* sp. bears the same field number (RHT 1304) as an isolated pinniped unciform, UCMP 315242 (formerly catalogued as UCR 15242) that was identified by Repenning and Tedford (1977:14) as a female of the odobenid pinniped *Aivukus cedrosensis* Repenning and Tedford, 1977.

DESCRIPTION. This partial left tympanic bulla is slightly smaller than both the holotype and referred bullae of *A. whistleri*, which it resembles by having the anterior portion of the medial part of its involucrum very thick, both transversely and dorsoventrally, and by having a prominent and ventrally bulging posterior part of the lateral part of the involucrum. It differs from both the holotype (UCMP 314589) and the referred (UCMP 324043) tympanic bullae of *A. whistleri* and from the specimen identified in previous text (UCMP 324044) as *Albireo* aff. *A. whistleri*, by being less massive, by having a less prominent and less squared posterior part of the involucrum, a less massive lateral part of the involucrum, a wider lateral groove, and smoother surface texture.

DISCUSSION. The unusual shape of this bulla indicates possible affinities with *A. whistleri*. Its differences, and the fact that it was derived from a stratigraphically higher source than any of the other albireonid specimens from Isla Cedros, suggest that it might represent a different species of *Albireo*. Its smaller size and lesser rugosity of its surface suggest that it might also belong to an ontogenetically younger individual. Combined with the other specimens that were found from horizons that are higher stratigraphically than the holotype, it provides an indication of an extended time interval during which dolphins resembling *A. whistleri* lived in the area of Isla Cedros.

Albireo savagei new species
Figures 31a–c, 32, 33a, 34; Table 4

"... as yet unnamed species of *Albireo* ..." Barnes, 1988a, 1988c:8A.

"... an undescribed species ..." Fordyce and Barnes, 1994:439.

DIAGNOSIS OF SPECIES. A species of *Albireo* differing from *A. whistleri* by having atlas vertebra larger, proportionally shorter anteroposteriorly, with longer and more slender transverse processes, larger neural canal, and more reduced remnant of transverse foramen; thoracic vertebrae proportionally and absolutely more elongate anteroposteriorly; longer first rib; greater arc of curvature of ribs; differing in body proportions from *A. whistleri* by having relatively shorter

neck, relatively longer thoracic region, and more voluminous thoracic cavity.

HOLOTYPE. UCMP 112048, partial skeleton of one individual, including atlas vertebra, thoracic vertebrae 4, 5, 6, 7, 8, and possibly 11, and parts of several ribs; collected by Donald E. Savage and Lawrence G. Barnes, 17 and 18 September 1970, L.G. Barnes field number 590.

TYPE LOCALITY. UCMP locality V-70148; in a road cut, approximately 1 m above the level of the road grade, across the road from the Union Oil Company pier, on the north side of the road that goes from Avila Beach to Port San Luis, Avila Beach, San Luis Obispo County, California, USA; on the Arroyo Grande, California, 15′ Topographic Map, U.S. Geological Survey, 1952 edition.

FORMATION AND AGE. The holotypic skeleton of *A. savagei* was collected from the Squire Member of the Pismo Formation, which is late Pliocene in age, approximately 3 to 2 Ma, and correlative with the Blancan North American Land Mammal Age (see Hall, 1973; Domning, 1978:75, 160). The stratum that contained the specimen is a coarse-grained, yellowish colored, firm but not indurated sandstone that contains rounded cobbles. Stratigraphically above this horizon is a white sandstone. Stratigraphically below the level that yielded the holotype of *A. savagei*, the yellow sandstone contains angular rock clasts, and this yellow sandstone grades downward into a greenish sandstone that disconformably overlies volcanic rocks.

The type locality of *A. savagei* and nearby localities in the same deposit have produced a small but important assemblage of fossil marine vertebrates and invertebrates: the late Pliocene pectinid *Lyropecten cerrosensis* (Gabb, 1866), an extinct grebe *Gavia* cf. *G. concinna* Wetmore, 1940, an unidentified otariine pinniped, a balaenopterid mysticete whale, the horse *Equus* sp., and the primitive relative of Steller's Sea Cow, *Hydrodamalis cuestae* Domning, 1978. The holotype (UCMP 86433) of *H. cuestae* was found at the same locality as the holotype of *A. savagei*, but from slightly higher stratigraphically within the section.

ETYMOLOGY. The species is named in honor of the late Dr. Donald E. Savage, formerly professor of paleontology, and director of the Museum of Paleontology, at the University of California, Berkeley. Dr. Savage helped me collect the holotype of *A. savagei*, and he was instrumental in having the specimen prepared for study and illustration.

DESCRIPTION. As the bones of this skeleton were removed from the sediment in the laboratory, they were given sequential numbers (1–26) to allow reference to their positions in notes and diagrams. These numbers are on the bones in ink within inked circles.

Among the bones of this partial skeleton, the atlas vertebra (Fig. 31a, laboratory label number 1) is the most complete, and the morphology of this bone is the most compelling reason for recognizing this as a member of the genus *Albireo*. The atlas very closely resembles that of the holotype of *A. whistleri* by being large, flattened and moderately compressed anteroposteriorly, and approximately oval shaped in anterior view and by having large but shallow anterior articular surfaces, a very small ventral tubercle positioned ventral to the small fossa that received the odontoid process of the axis vertebra, anteroposteriorly aligned rugosities on the ventral surface of the centrum, and a relatively large, single, elongate, laterally directed transverse process.

Compared with the atlas of *A. whistleri* (Fig. 31d), that of *A. savagei* (Fig. 31a) differs by being absolutely and relatively taller, wider, and having a dorsoventrally higher neural canal. Its transverse processes project farther laterally and are not so expanded in an anteroposterior plane. The atlas of *A. savagei* is, however, both measurably and proportionally thinner anteroposteriorly than that of *A. whistleri* (Table 4).

Its anterior articular surfaces are broad and shallow, as are those of *A. whistleri* (compare Fig. 31a and 31d), indicative of similarly wide but not prominently projecting occipital condyles on the cranium. The posterior articular surfaces are asymmetrical both in size and shape: The left posterior articular surface has a uniform crescentic outline, but the right articular surface extends laterally onto the base of the transverse process. The opposite is the case on the holotypic atlas of *A. whistleri*: Its left articular surface extends laterally onto the base of the transverse process. These asymmetries in both known specimens suggest that there was a tendency for pathologies in the atlas and axis vertebrae of *Albireo* (see Thomas et al., 2008).

In both species of *Albireo*, the intervertebral foramen, which is located dorsal to the anterior articular surface, is incompletely formed. It is represented by a transverse sulcus bordering the dorsal margin of the articular surface, and the atrophy of the dorsal part of this foramen is a derived character. In *A. whistleri*, the margin of the articular surface extends dorsally to mark the anterior wall of this foramen; however, in *A. savagei*, this articular surface does not extend so far dorsally. The latter is the more derived character state, indicating less definition of the foramen.

On the basis of its proportionally greater anteroposterior compression, the atlas vertebra of *A. savagei* is more derived than that of *A. whistleri.* This is consistent with the trend in various delphinoid lineages for progressive anteroposterior shortening of the cervical vertebrae. Its relatively longer transverse processes might be

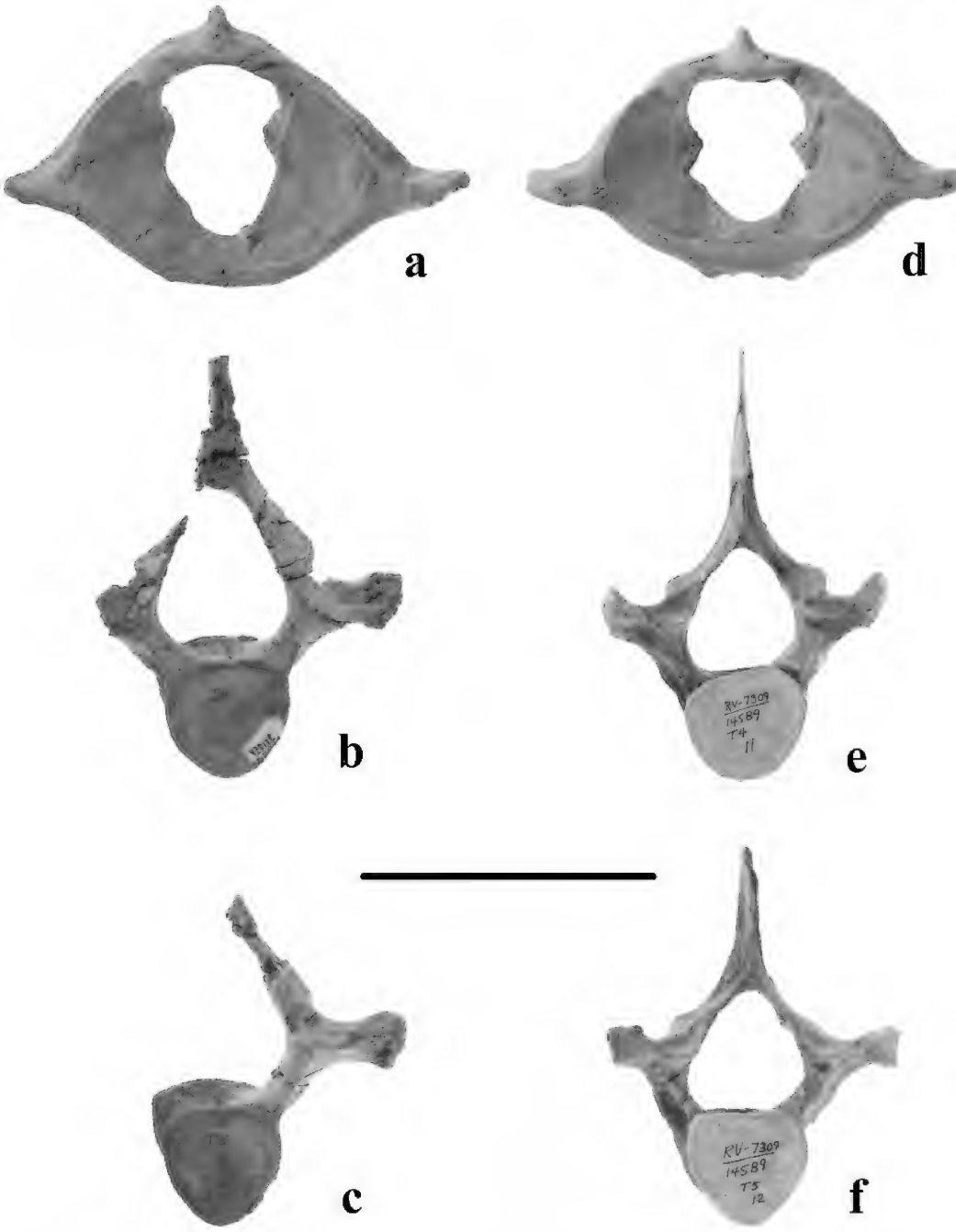

Figure 31 Vertebrae, in anterior views, of two species of *Albireo* Barnes, 1984a. **a–c**, *Albireo savagei*, sp. nov., holotype, UCMP 112048, from Avila Beach, San Luis Obispo County, California, USA: **a**, atlas vertebra; **b**, fourth thoracic vertebra; **c**, fifth thoracic vertebra; **d–f**, *Albireo whistleri* Barnes, 1984a, holotype, UCMP 314589, from Isla Cedros, Baja California, Mexico; **d**, atlas vertebra; **e**, fourth thoracic vertebra; **f**, fifth thoracic vertebra. Scale bar = 10 cm.

considered to be a primitive character state because the transverse processes are elongate in the Archaeoceti (see Kellogg, 1936:fig. 10). However, in the case of the evolution of *Albireo*, it is most likely that the transverse processes have become secondarily re-elongated in *A. savagei*. This conclusion is based on the relatively shorter transverse processes on the atlas vertebra of *A.*

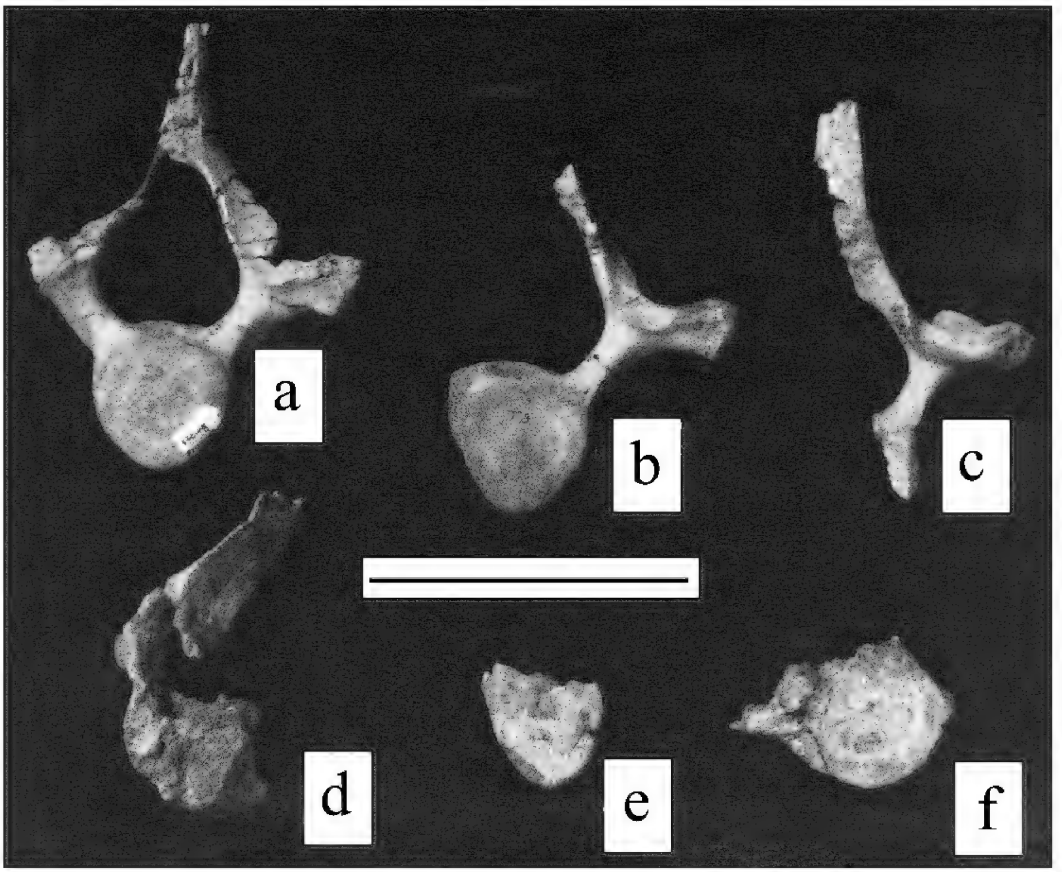

Figure 32 *Albireo savagei*, sp. nov., holotypic thoracic vertebrae in anterior views, UCMP 112048, from UCMP locality V70148, Avila Beach, San Luis Obispo County, California, USA: **a**, anterior view of fourth thoracic vertebra; **b**, anterior view of fifth thoracic vertebra; **c**, anterior view of possible sixth thoracic vertebra; **d**, anterior view of possible seventh thoracic vertebra; **e**, anterior view of possible eighth thoracic vertebra; **f**, anterior view of possible 11th thoracic vertebra. Scale bar = 10 cm.

whistleri that are approximately of the same proportion as they are on the atlas vertebra of *K. pernix* (see Kellogg, 1927:pl. 12, figs. 3 and 4). It is logical to assume that middle Miocene *K. pernix* represents more primitive delphinoid morphology than the geochronologically younger and morphologically more derived members of the family Albireonidae. The transverse processes of both species of *Albireo* project horizontally away from the body of the vertebra, and this is a derived character state compared with the situation in *K. pernix*, in which the transverse processes of the atlas vertebra are oriented ventrolaterally.

The series of preserved thoracic vertebrae of the holotype of *A. savagei* includes no complete vertebra, but each vertebra is suitably complete so that the vertebrae may be arranged in a sequence in which the vertebral centra increase progressively in thickness proceeding from anterior to posterior. Judging by the similar vertebrae in the holotypic skeleton of *A. whistleri*, this sequence of vertebrae includes thoracic vertebrae 4 through 8, and possibly 11. Each of these vertebrae is absolutely and proportionally longer anteroposteriorly than its apparent counterpart in *A. whistleri*.

During maturation of cetaceans, the vertebral epiphyses begin to fuse to the vertebral centra at both the anterior and posterior ends of the vertebral column, and this phenomenon moves progressively toward the middle of the vertebral column. This age-related phenomenon of epiphysis fusion indicates that the individual represented by the holotype of *A. savagei* was more mature at its death than was the holotype of *A. whistleri*.

The fourth thoracic vertebra of *A. savagei* (Figs. 31b and 32a, laboratory label number 7) resembles that of *A. whistleri* by having a centrum that narrows ventrally with concave lateral sides and by having the laminae (or pedicles) directed anterodorsally and bearing large and well-formed prezygapophyses and postzygapophyses. The floor of its neural canal

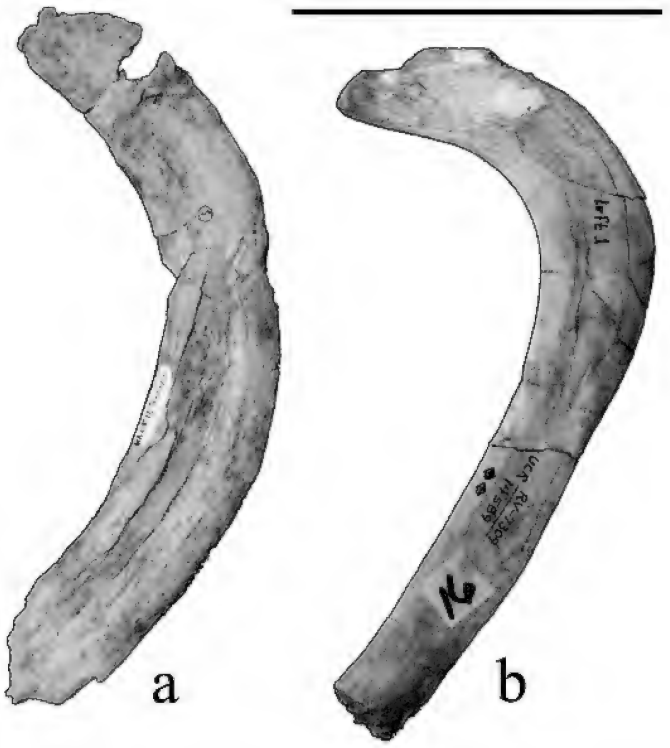

Figure 33 First left ribs, in anterior views, of two species of *Albireo* Barnes, 1984a: **a**, holotype of *Albireo savagei*, sp. nov., holotype, UCMP 112048; **b**, holotype of *Albireo whistleri* Barnes, 1984a, UCMP 314589. Scale bar = 10 cm.

is similarly concave, but it bears one foramen rather than two. The fovea for the rib at the end of the transverse process of this vertebra is large and wide, and the dorsal process is elongate and slants posteriorly. Its vertebral epiphyses are fully fused to the centrum, whereas in the less mature holotype of *A. whistleri*, the epiphyses of this vertebra are loose from the centrum. In addition to being larger, the fourth thoracic vertebra of *A. savagei* differs from that of *A. whistleri* (compare Fig. 31b and 31e) by having longer and anteroposteriorly wider transverse and neural processes and an anteroposteriorly more elongate centrum.

The probable fifth thoracic vertebra of *A. savagei* (Figs. 31c and 32b, labeled number 6) is larger than the previous vertebra, and it has a more anteroposteriorly elongate centrum. It fits properly against the posterior side of the fourth thoracic vertebra. It resembles the fifth thoracic vertebra of *A. whistleri* (compare Fig. 31c and 31f) by having a centrum that narrows ventrally and is concave laterally and by having the laminae (or pedicles) directed anterodorsally and bearing large and well-formed prezygapophyses and postzygapophyses. The ventral surface of its neural canal is similarly concave, and it likewise bears one foramen. The fovea for the rib at the end of the transverse process is very large and wide, and the preserved base of the dorsal process is wide and slants posteriorly. Its vertebral epiphyses are fully fused to the centrum, whereas in the less mature holotype of *A. whistleri*, the epiphyses of this vertebra are loose from the centrum. In addition to being larger, the fifth thoracic vertebra of *A. savagei* differs from that of *A. whistleri* by having more massive, longer, and anteroposteriorly wider transverse and neural processes and an anteroposteriorly longer centrum.

An incomplete vertebra (laboratory label number 8) that is possibly the sixth thoracic vertebra of *A. savagei* (Fig. 32c) has a more anteroposteriorly elongate centrum and a wider neural process than the previous vertebra. It does not fit as well as would be expected against the posterior side of the fifth thoracic vertebra, but it is definitely in a more posterior position in the vertebral column than the previously described vertebra. It resembles the sixth thoracic vertebra of *A. whistleri* by having a centrum that has concave lateral sides, but it has a lamina that is directed more dorsally. The fovea for the rib at the end of the transverse process is not completely preserved.

The partial vertebra (laboratory label number 24) that is possibly the seventh thoracic vertebra of *A. savagei* (Fig. 32d) has a more

Figure 34 *Albireo savagei*, sp. nov., holotypic ribs, UCMP 112048, from UCMP locality V70148, Avila Beach, San Luis Obispo County, California, USA, anterior views of ribs beginning with the first rib at the left side, with progressively more slender ribs that appear to represent much of the rib cage on the left side of the skeleton. Scale bar = 10 cm.

elongate centrum than the previously described vertebra and an anteroposteriorly wider dorsal process. Because of the variably incomplete preservation of the two vertebrae, there is no possible articulation between them, but this vertebra definitely is from a more posterior location in the vertebral column than the previous one. It resembles the sixth thoracic vertebra of *A. whistleri* by having a centrum that has a concave lateral side, but it is consistent with being more posterior in the vertebral column than thoracic vertebra 6 by having a lamina that is directed more dorsally, an anteroposteriorly wider dorsal process, and a centrum that is more elongate anteroposteriorly and has a less concave lateral side. Its epiphyses are not fused to the vertebral centrum.

The partial vertebral centrum (laboratory label number 9) that is possibly the eighth thoracic vertebra of *A. savagei* (Fig. 32e) has a centrum similar in length to the previously described vertebra, but it apparently is from a location more posterior in the vertebral column, because its lateral surface is less concave.

The next vertebra in the sequence (laboratory label number 13) appears not to be the one that immediately follows the previous vertebra because of the much greater anteroposterior length of its centrum (Fig. 32f). Its centrum is also wider and has a sharp ventral keel, and its pedicle and transverse process are much wider anteroposteriorly. In life, its anterior epiphysis was not fused to the vertebral centrum. It is probably from the posterior part of the thorax and resembles the 11th thoracic vertebra of *A. whistleri*, but it has an anteroposteriorly longer centrum.

The holotypic partial skeleton of *A. savagei* has parts of several ribs. Calculating by the parts of ribs that include the tubercle or the capitulum, possibly as many as 10 or 11 ribs are represented with this specimen.

The first left rib (Fig. 33a, laboratory label number 3) is represented and, similar to the corresponding rib of *A. whistleri*, it is exceptionally wide transversely and very flattened anteroposteriorly. It differs from the first rib of *A. whistleri* (Fig. 33b) by being longer and by having a greater arc of curvature relative to the sagittal plan of the body. This indicates that the thoracic cavity of *A. savagei* was more voluminous than that of *A. whistleri.*

Three parts (laboratory labels number 4 and 20) of what appear to be the second left rib are present.

Like the second rib of *A. whistleri*, these rib parts differ from the first rib by having a longer neck and by being less expanded transversely. They differ from the second rib of *A. whistleri* by having a larger capitulum and tuberculum and by being broader distally. The articular facet on the tuberculum slopes posteroventrally, and this is consistent with its being a left rib.

Parts of at least 10 other ribs are with the holotype of *A. savagei* (Fig. 34), all from positions more posterior in the body than the second rib. They are too fragmentary to identify in detail. The proximal ends that are preserved of ribs from the midthoracic region have elongate and narrow capitula that are separated from the tubercula.

CONCLUSIONS

1. Species in the extinct odontocete cetacean family Albireonidae are very rare, medium-sized, fossil dolphins that are known only from temperate latitudes around the margin of the eastern North Pacific Ocean. Their fossils have been found in Baja California in Mexico, in California, USA, and on Hokkaido, Japan. The known geochronologic range of the family Albireonidae is from the late Miocene, approximately 9 million years ago, to the late Pliocene, approximately 2 or 3 million years ago.
2. The family Albireonidae is classified in the superfamily Delphinoidea and is presently monogeneric, including only the genus *Albireo* Barnes, 1984a. *Albireo* is represented by two named species from the eastern North Pacific. These are: latest Miocene *Albireo whistleri* Barnes, 1984a, from Baja California, Mexico, and late Pliocene *Albireo savagei*, sp. nov., from central California, USA.
3. *Albireo whistleri*, from the basal part of the Lower Member of the Almejas Formation on Isla Cedros, Baja California, Mexico, is latest Miocene in age, approximately 6 to 8 million years old. The holotypic skeleton is missing the caudal vertebrae, chevron bones, and some of the phalanges, but is one of the most complete fossil cetacean skeletons ever collected.
4. Some isolated tympanic bullae from stratigraphically higher levels of the Lower Member of the Almejas Formation on Isla Cedros represent *A. whistleri* and less specifically identifiable taxa: *Albireo* aff. *A. whistleri* and *Albireo* sp. These bullae, from higher stratigraphic levels in the Almejas Formation, are progressively more different morphologically from the holotypic bulla of *Albireo whistleri*. These fossils indicate that albireonids lived along the west coast of Mexico for a considerable period of time, and corroborate other evidence that a considerable period of time is represented by the strata within the Lower Member of the Almejas Formation on Isla Cedros.
5. The geochronologically younger species, *Albireo savagei*, was found at Avila Beach, San Luis Obispo County, California, in the Squire Member of the Pismo Formation, and is of late Pliocene age, approximately 2 to 3 million years old. The holotype and only known specimen of this species includes the atlas vertebra, thoracic vertebrae, and ribs of one individual. *Albireo savagei* differs from *A. whistleri* by being larger and by having a relatively more anteroposteriorly compressed atlas vertebra, a larger thoracic cavity, and relatively more elongate thoracic vertebrae, the latter being a more primitive character state. The existence in this later species of the more primitive character state suggests either an evolutionary reversal or the existence of at least two lineages within the family Albireonidae.
6. *Albireo whistleri* has a combination of cranial characters that is unlike that possessed by any species of odontocete in any of the other families within the superfamily Delphinoidea. The overall shape of the cranium is very much like that of the highly derived, living Dall's Porpoise, *Phocoenoides dalli* (family Phocoenidae). Other characters of *A. whistleri* that define the family Albireonidae are: large brain case, dorsally curved rostral extremity, raised eminences on the premaxillae anterior to the narial openings, wide and flat posterior premaxillary terminations, wide and flat nasal bones, wide and flat exposures of the frontal bones on the cranial vertex, frontal bones (instead of the nasal bones) comprising the highest part of the cranial vertex, mesorostral groove closed dorsally in the proximal two thirds of the rostrum, thick lateral margin of the maxilla, large orbits, absence of a supraorbital lobe of the pterygoid air sinus, large and globose petrosal with a large cochlear portion, homodont dentition, teeth with smooth enamel and conical crowns, unfused and relatively long mandibular symphysis that equals approximately one third of the length of the dentary, relatively wide basihyal and thyrohyal, anteroposteriorly shortened cervical vertebrae, ankylosed second and third cervical vertebrae, increased numbers of thoracic and lumbar vertebrae which have anteroposteriorly compressed centra and elongate transverse and dorsal processes, relatively wide first rib, anteroposteriorly narrow and proximodistally expanded blade of the scapula, humerus expanded anteroposteriorly at its distal end, radius with the distal end broad and anteroposteriorly much expanded, and ulna that is short and anteroposteriorly expanded.

7. The nearly complete holotypic skeleton of *A. whistleri* made possible a reconstruction of the body skeleton and of the animal in the flesh. In life, *A. whistleri* was approximately the size of a living bottlenose dolphin (*T. truncatus*); thus, it was by present day standards, a medium-sized dolphin, approximately 2.5 m long. It probably had a large melon and a somewhat flexible neck, was dorsoventrally deep in the thorax, and had anteroposteriorly expanded pectoral flippers. The sizes and shapes of its dorsal fin and caudal fluke are conjectural.

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Examples of paleopathologies in some fossil Cetacea from the North Pacific realm

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ABSTRACT. Fossil cetacean bones from various localities worldwide exhibit damage and modifications resulting from disease and injury. Examples of cetacean osteological pathologies have been found in Tertiary age marine deposits bordering the eastern North Pacific Ocean. A pathology involving two joined mysticete thoracic vertebrae from the upper Oligocene Pysht Formation in Washington is likely the result of the anterior vertebra having been crushed in life, followed by the two vertebrae rubbing against each other, causing a large callus. Abundant examples of cetacean paleopathology are from the middle Miocene Sharktooth Hill Bonebed in Kern County, California. A caudal vertebra of a large mysticete was broken in a dorsoventral plane, probably from impact with a solid object, perhaps a rock or another whale. Subsequent to healing, however, there was damage from a bacterial infection similar to *Brucellosis*, a bacterium that could have entered the body through a laceration when the vertebra was broken. Other pathologic mysticete bones from the Sharktooth Hill Bonebed include fused caudal vertebrae, cervical vertebrae with lipping, and ribs with healed fractures. Forelimb bones of the sperm whale, *Aulophyseter morricei*, show fusion and osteophytes. An axis vertebra of a large dolphinlike odontocete has idiopathic breakage of its posterior vertebral epiphysis, subsequent healing, and extensive osteophytosis around the injury. Vertebrae, probably of small kentriodontid dolphins, exhibit asymmetry, bony lesions, and osteophytes. Several humeri of probable kentriodontid dolphins show myositis ossificans traumatica and bone deformation at the ulnar facet, as well as osteophytes around the distal articulations for the ulna and radius. A dolphin humerus from the late Miocene Monterey Formation in Orange County, California, has myositis ossificans traumatica, possibly resulting from a torn tendon in the proximal part of its fore flipper. The holotype of the primitive phocoenid porpoise, *Piscolithax tedfordi*, from the latest Miocene Almejas Formation on Isla Cedros, Baja California, Mexico, exhibits effects of possible osteoarthritis in both foreflippers. At the time of death, its disease was sufficiently advanced that the right humerus and ulna were fused together. This probably did not affect its swimming abilities because the elbow joints of all modern Cetacea, although not normally fused, are structurally rigid. The holotype of the albireonid delphinoid *Albireo whistleri*, also from the Almejas Formation on Isla Cedros, has apparently congenital asymmetry of its atlas vertebra. Similar asymmetry exists in the holotypic atlas vertebra of *Albireo savagei* Barnes, 2008, from the Pliocene Pismo Formation in central California. Importantly, each of these individuals survived its ailment for a considerable period of time—even the dolphin with a broken axis vertebral epiphysis. Similar pathologies exist among Recent cetaceans, and such maladies clearly have afflicted these marine mammals for much of their evolutionary history.

INTRODUCTION

Bone pathologies are well preserved and easily recognized in fossils; indeed, they are the primary evidence of pathology in the fossil record of extinct vertebrates. The study of paleopathology is relatively voluminous, but it has not been uniform among various groups. Bone pathologies

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are relatively frequent among Recent marine mammals, and we have found them to be similarly present among diverse fossil marine mammals as well. For example, paleopathologies have been found in the allodesmine otarioid pinniped *Allodesmus* Kellogg, 1922 (Barnes, 1972), and in the dusignathine otarioid pinniped *Gomphotaria pugnax* Barnes and Raschke, 1991 (see Barnes and Raschke, 1991; Thomas and Barnes, 2001; and Barnes, Thomas, and Raschke, 2002).

A few examples of fossil cetacean osteological pathologies have been reported previously, some of which are reviewed below. The purpose of this study is to document several additional occurrences of bone pathologies among fossil cetaceans from the west coast of North America and to attempt to attribute causes to some of these pathologies. Some of these were reported in a preliminary fashion by Thomas and Barnes (2002). We hope that this study will promote the observations and descriptions of other such examples from the fossil record. We list the examples in geochronologic sequence of their occurrences, from oldest to youngest.

SOME PREVIOUSLY REPORTED CETACEAN PALEOPATHOLOGIES

Pathologies have been noted in taxonomic or descriptive studies of fossil cetaceans; however in most instances, the reason for the pathology was not determined or suggested. In the late Eocene, Egyptian basilosaurid archaeocete *Dorudon atrox* (Andrews, 1906), Uhen (2004:183, figs. 139–140) has shown exostoses on vertebrae, fusion of vertebrae, and healed fractures of ribs.

Rothschild and Sanders (1997) reported avascular necrosis (also called osteonecrosis), resulting from "the bends," in bones of various fossil whales ranging from Oligocene to Pliocene in age. They did not find this particular pathology in Recent cetaceans, and they concluded that evolutionary developments had permitted more modern whales to cope with the problem. However, Moore and Early (2004) have subsequently reported bone damage, apparently caused by the bends, in Recent sperm whales, animals that are known to dive repeatedly to great ocean depths.

Dawson (1996) documented a partial dolphin skeleton, from the Calvert Formation of Maryland, which she referred to the large middle Miocene kentriodontid delphinoid *Hadrodelphis calvertense* Kellogg, 1966. Dawson's (1996) paper was primarily taxonomic and morphologic, but she did note that the animal had some bone pathologies. Subsequently, Dawson and Gottfried (2002) described the numerous pathologies in this skeleton: two ribs with healed fractures, two vertebrae with idiopathic vertebral spondylosis, and chronic osteomyelitis in the right mandible. In addition to those pathologies, we think that what Dawson (1996) referred to as the deltopectoral crest of the humerus is also a pathology, an exostosis. This is because six of the 11 pathologic kentriodontid dolphin humeri that we document in the following text have an exostosis at the same location on the humerus, but many more kentriodontid humeri from the Sharktooth Hill Bonebed do not exhibit this same enlarged tubercle, and we believe those humeri have the normal condition. The exostoses that are present on the various humeri from the Sharktooth Hill Bonebed are of different sizes and shapes, but they are all at the same location on each of these humeri.

Osteological pathologies in the skeleton of a middle Miocene mysticete from Virginia were alluded to in the species name of *Thinocetus arthritus* Kellogg, 1969. The holotype of this species has on its third through 10th dorsal vertebrae what Kellogg (1969:13) called spondylitis deformans or osteophytosis. Rothschild and Martin (1993:238) subsequently diagnosed the condition in this same specimen as being diffuse idiopathic skeletal hyperostosis.

Kellogg (1969:20, fig. 12) mentioned the presence of raised margins around the posterior vertebral epiphysis of the third cervical vertebra of the middle Miocene mysticete *Pelocetus calvertensis* Kellogg, 1965, from the Calvert Formation in Maryland. These modifications are similar to hyperostotic lipping around vertebral epiphyses that we report in the following text.

The atlas vertebra of the holotype of the bizarre tusked late Miocene odontocete from Peru, *Odobenocetops leptodon* Muizon, Domning, and Parrish, 1999, has extensive pathologies on its atlas vertebra. The articular facets for the occipital condyles of the cranium both have osteoarthritic lipping around their entire margins (see Muizon and Domning, 2002:fig. 11; and for a similar condition see also Aufderheide and Rodríguez-Martín, 1998:93–94). On the specimen of *O. leptodon*, a fold in the bone in the left articular surface near the neural canal is similar to a fold that exists in two cetacean specimens (Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County [LACM] 151236 and LACM 115127) from the Sharktooth Hill Bonebed that we describe in the following text. All three of the specimens from the Sharktooth Hill Bonebed have the fold on the left articular facet. On the holotypic atlas of *O. leptodon*, the surfaces of both articular facets are roughly textured and pitted, and the pitting is most profound laterally and dorsally. There is a prominent pit at the approximate midlevel of each facet is adjacent to

the neural canal. The pit in the left facet is the dorsal termination of the fold that was previously mentioned. There is also an indentation in the left facet near its lateral edge, and a growth on the left posterior side of the neural arch. This growth created a complete circle surrounding the left transverse foramen, which is much larger than the right transverse foramen which, although not enclosed completely, does have a much more constricted opening. Muizon and Domning (2002:437) noted the asymmetry in the atlas vertebra of *O. leptodon*, especially of the posterior articular facet, which they suggested might be related to the asymmetrically larger right tusk of the animal. In addition, the posterior articular surfaces of the atlas have lipping (osteophytes) around their edges, rough texture, and the crestlike folds, all of which are consistent with vertebral osteophytosis (see Aufderheide and Rodríguez-Martín, 1998:96). The same type of osteoarthritic lipping is also around the facet for the dens.

The humerus of the short-snouted pontoporiid dolphin, *Brachydelphis mazeasi* Muizon, 1988, also from the Pisco Formation in Peru, has extensive bone deformation, rugose bone growth, and bone resorption (see Muizon, 1988:126).

METHODS AND MATERIALS

Our identifications and diagnoses of the cetacean paleopathologies are based on the work of Jaffe (1972), Ortner and Putschar (1985), Rothschild and Martin (1993), and Aufderheide and Rodríguez-Martín (1998). Although cetacean pathologies were not the subject of these studies, we decided to employ the most applicable terminologies provided therein to describe the pathologies that we observed in fossil cetaceans.

ABBREVIATIONS

Specimens cited here are housed in the following institutions, as indicated by the following abbreviations:

LACM	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
UCR	Department of Geological Sciences, University of California, Riverside, California; collections and records now maintained at the Museum of Paleontology, University of California, Berkeley, California USA
UWBM	Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington USA

PALEOPATHOLOGIES OF SOME NORTH PACIFIC FOSSIL CETACEA

EXAMPLE FROM THE LATE OLIGOCENE PYSHT FORMATION

Geology and Age

The middle to late Oligocene part of the Pysht Formation is exposed on the south side of the Strait of Juan de Fuca on the north shore of the Olympic Peninsula, Washington. A diverse assemblage of fossil marine vertebrates occurs in the upper part of the Pysht Formation in this area, and vertebrates in this assemblage have been reported by Olson (1980), Domning et al. (1986), Ray et al. (1994), Barnes and Goedert (1996, 2001, 2002), and Barnes, Goedert, and Furusawa (2002). Small tooth-bearing aetiocetid mysticetes (Barnes et al., 1995; Goedert et al., 2004), some baleen-bearing mysticetes (Crowley and Barnes, 1996), and a diversity of odontocetes (Barnes and Goedert, 1996; Barnes, Goedert, and Furusawa, 2002) have been reported from this horizon, but to date, no cetacean as large as the following specimen has been identified in the fossil marine mammal assemblages from the Pysht Formation.

Suborder Mysticeti Flower, 1865

Genus and Species Undetermined

MATERIAL. UWBM 87106, two fused vertebrae collected from UWBM locality C0758.

DISCUSSION. This specimen was previously reported by Thomas and Barnes (2002). The vertebrae (Fig. 1A–1C) are of a size that indicates the animal had, in life, a total body length of approximately 8 m. The specimen most likely represents a mysticete, and judging by its size, it was probably a baleen-bearing mysticete. It would be a small to medium-sized mysticete compared with living cetaceans.

The specimen consists of two sequential thoracic vertebrae. The anterior of these two vertebrae exhibits idiopathic crushing (Fig. 1A). Both vertebrae exhibit large calluses on the ventral edges of their centra that are consistent with calluses in fractures that have been reported by Aufderheide and Rodríguez-Martín (1998:20) (and see Fig. 1A–1C) and which were probably caused by the ventral edges of the centra rubbing together during the natural motion of the whale while swimming. The crushed anterior vertebra is angled at a slight tilt toward the right side of the body. The calluses are developed primarily on the ventral right side of the two vertebrae (Fig. 1C), which is consistent with the tilt having developed during the life of the whale, rather than having been caused by geologic compression. With the bones at a slight angle to each other, the two vertebrae would have rubbed against one an-

other, thereby generating a callus that would be consistent with what exists in this specimen. A callus this large would have taken considerable time to develop. Whether the injury was the result of a trauma or from repeated diving to depths with high water pressures, the whale survived for a long time with this injury, and it was probably not the cause of its death.

EXAMPLES FROM THE MIDDLE MIOCENE SHARKTOOTH HILL BONEBED

Geology and Age

The middle middle Miocene Sharktooth Hill Local Fauna (Barnes, 1977) produced the majority of examples of fossil cetacean pathologies that we report herein. The local fauna is derived from the Sharktooth Hill Bonebed (see Barnes, 1977:326–327), a horizon that is widely exposed in outcrops of the Round Mountain Silt in the area northeast of Bakersfield in Kern County, California. The age and stratigraphic relationships of the upper part of the Round Mountain Silt, which includes the bonebed, are well known, is approximately 15.3 Ma, and is correlated with the Temblor Provincial megainvertebrate stage of Addicott (1972), the Relizian and/or Luisian foraminiferal stages, and the Barstovian North American Land Mammal Age (Barnes, 1977; Barnes and Mitchell, 1984; Barnes et al., 1999; Prothero et al., in press).

Suborder Mysticeti Flower, 1865

Genus and Species Undetermined

COMMENTS

Three species of extinct mysticete cetaceans were named from this bonebed by Kellogg (1931). On the basis of isolated cranial parts, petrosals, and tympanic bullae, they are: *Parietobalaena securis* Kellogg, 1931; *Tiphyocetus temblorensis* Kellogg, 1931; and *Peripolocetus vexillifer* Kellogg, 1931. Kellogg assigned all three to the family Cetotheriidae. Such family assignments were commonly made at that time for many fossil mysticetes but would now be considered suspect. The true identities of Kellogg's mysticetes from the Sharktooth Hill Bonebed remain problematic, even while the Sharktooth Hill Local Fauna has become a standard of comparison for middle Miocene marine vertebrate assemblages worldwide. In addition to the three named species, there are other mysticetes in the local fauna (Barnes, 1977:327; Barnes et al., 2005), none of which is presently identified at the species level and none of which is known by postcranial bones. Therefore, the mysticete fossils described herein are not precisely identified.

Pathologic Caudal Vertebra

MATERIAL. LACM 151218, caudal vertebra collected by Howell W. Thomas in 1979 from locality LACM 3162.

DISCUSSION. This example (Fig. 2A–2D) is from a large mysticete that was larger than any of the three that Kellogg (1931) named in the Sharktooth Hill Local Fauna. It was previously reported by Thomas and Barnes (2002) and shows two apparently related pathologies. On the basis of comparisons with the middle Miocene mysticete from Virginia, *Thinocetus arthritis* Kellogg, 1969, LACM 151218 is probably a fourth or fifth caudal vertebra: It has a small transverse process with a transverse foramen, and a small dorsal process (see also Kellogg, 1969:pl. 13, figs. 4 and 5).

The centrum of this vertebra was broken in a dorsoventral plane (Fig. 2B-1), probably from impact with a solid object, and it subsequently healed. It also has damage, apparently from a bacterial infection, that could have been introduced into the body through a cut at the time that the vertebra was broken. The effects of the bacterial infection are deep pitting in the anterior vertebral epiphysis (see Fig. 2A-1 and for similar examples see Aufderheide and Rodríguez-Martín, 1998:192). Multiple pitting forms one large pit; the largest pit being approximately 28 mm deep, which penetrates through the vertebral epiphysis into the vertebral centrum. The overall pitted area is approximately 70 mm in diameter.

The epiphyses of this vertebra were firmly fused to the centrum, and the sutures are obliterated; thus, the individual was fully mature when it died. Healing of the break is evidenced by the growth of bone that now covers both the dorsal and ventral edges of the fissure. A small crack can be seen on the anterior side of the centrum, indicating that the break originally extended entirely through the vertebra. The entire exterior face of the centrum exhibits altered bone development that is consistent with a *Brucellosis* type of bacterial infection (Fig. 2C and 2D and, for a similar example, see Aufderheide and Rodríguez-Martín, 1998). The ventral exterior face of the centrum exhibits erosive bone deformation, with two extensive pits (Fig. 2D). The dorsal process of this vertebra has been eroded, and there is extensive pitting into the anterior region, with eight well-developed pits on the dorsal surface of the centrum (Fig. 2C).

The centrum of this vertebra has hyperostotic lipping around the right side of its anterior section (Fig. 2A-2) and, to a lesser extent, along the lower left side (Fig. 2A-3). There is also hyperostotic lipping along the ventral left edge of the posterior section of the centrum, as well as on the central left edge, the ventral right corner, and the middle right edge (Fig. 2B-2). Demonstrating that the whale survived the injury, new bone had completely grown over the edges of the break (Fig. 2B-3).

The behaviors of living balaenopterid mysticetes might provide insight into a possible cause of such a major bone fracture as is present in this vertebra. Living small to midsized balaenopterids approach quite closely to rocky shorelines where the offshore water depth is sufficient. The Miocene whale could have approached too closely to a rocky shoreline, and its flukes could have struck a submerged rocky outcrop. Alternatively, living mysticetes are known to be aggressive in competitive aggregations during mating. A slap of the tail flukes could have resulted in the fracture exhibited by the vertebra from the Sharktooth Hill Bonebed. However, the possible bacterial infection, which we suspect resulted from a laceration, would agree more with the scenario of the whale having hit a rock rather than another whale.

Pathologic Cervical Vertebrae

MATERIAL. LACM 121493, two associated cervical vertebrae collected by Robert L. Clark in 1977 from locality LACM 3160; LACM 151230, axis vertebra collected by a LACM field party in 1973 from locality LACM 1625; LACM 151247, cervical vertebra collected by Joseph F. Arndt from locality LACM 6688.

DISCUSSION. LACM 121493 consists of two associated cervical vertebrae (Fig. 5A–5G). The specimen shown in Figure 5A–5D is probably a third cervical vertebra, judging by its close resemblance to the third cervical of the middle Miocene mysticete *Halicetus ignotus* Kellogg, 1969, from the Choptank Formation in Maryland (see Kellogg, 1969:pl. 17, fig. 5). Like the third cervical of *H. ignotus*, the vertebra LACM 121493 has a relatively low and broad neural canal and a thick and rugose lateral part of the transverse process that was in life closely appressed to the transverse process of the axis vertebra. The other vertebra (Fig. 5E–5G) is probably the sixth cervical vertebra. It resembles the sixth cervical vertebra of *H. ignotus* by having a relatively low and broad neural canal and a long, rodlike transverse process that curves ventrolaterally.

The apparent third cervical vertebra of LACM 121493 has multiple sites of osteophytes (e.g., see Rothschild and Martin, 1993:24) on the anterior and the posterior edges of its centrum (Fig. 5A and 5B). There are multiple bone deformations on the dorsal surfaces of both transverse processes. The irregularities on the transverse processes are involved with the close ligamental attachments to the transverse processes of the axis vertebra and are probably not pathologies. The probable sixth cervical vertebra (Fig. 5E–5G) has hyperostotic bone growth along the posterior margins of the lamina leading to the spinous process (Fig. 5F and 5G-1). The right superior and inferior articular surfaces are significantly larger than are the articular surfaces on the left side (Fig. 5G). There is a bony growth on the right side of the spinous process (Fig. 5F). There is also a bony growth on the left transverse process that measures 5 mm in diameter and approximately 3 mm high (Fig. 5G), and this is significantly larger than the corresponding growth on the right side. The dorsal process of this vertebra bends asymmetrically to the right side.

LACM 151230 (Fig. 5H) is an axis vertebra that probably belongs to the same species of mysticete as the previous specimen (LACM 121493) because the third cervical vertebra of that specimen fits appropriately onto this axis. It has a bone depression in the left midsection of the posterior side of the centrum. This depression appears to have been formed in response to something that was slowly invading the cartilage adjacent to the vertebra because the bone surface is smooth rather than pitted and shows interior bone. The smooth bone indicates that the bone had time to reabsorb and to heal as the depression continued to develop.

Another cervical vertebra, LACM 151247, has an osteophyte on the dorsal edge of the posterior end of its centrum.

Pathologic Caudal Vertebra

MATERIAL. LACM 151229, caudal vertebra collected at locality LACM 1625.

DISCUSSION. This is the caudal vertebra of a small mysticete, and because it has roundly convex epiphyses on each end, it is the vertebra that is at the point of flexion in the caudal peduncle of a whale. It has hyperostotic bone growth on the middorsal surface that increased the height of the vertebra around the dorsal process. Anterior to this area, it also has an area of absorptive bone degeneration of idiopathic origin in the left anterior dorsal region (Fig. 8F).

Pathologic Ribs

MATERIAL. LACM 48876, part of a rib collected by Edward D. Mitchell, Jr., in 1960 at locality LACM 1557; LACM 49941, partial rib possibly from locality LACM 6688; LACM 150323, section of rib collected by Howell W. Thomas in 1979 at locality LACM 3162.

DISCUSSION. LACM 48876 is the distal portion of a broken rib that has a callus that formed at the site of the break. After being broken, this section of the rib did not regrow to the proximal portion of the rib (Fig. 3A). LACM 49941 is a section of a rib, probably from a mysticete, that has a large callus that developed at the site of a healed break. LACM 150323 is another rib of a large cetacean, also most likely a mysticete. Its position was in the posterior half of the thoracic cavity because it has a tubercle but

no capitulum, and such ribs are in the posterior part of the thorax of cetaceans (Winge, 1942:248). Extra bone growth is present at the area of curvature at the proximal part of this rib. The distal part of the rib, near a postmortem break, appears normal in texture, and is typically subquadrate in its cross section. The affected part of this rib has irregular bony growths that appear to have resulted from an oblique fracture across the proximal part of the rib (Fig. 3B). Such a break could have resulted from a blow to the thoracic cavity that compressed the body of the animal. During feeding, courtship, mating, and display, living mysticetes are known to leap far out of the water, sometimes in close proximity to one another. The animal that had this rib could have landed on another whale, or another whale could have landed on it and, in either case, the thoracic cavity could have sustained a vertical blow that could account for this break.

Pathologic Scapula

MATERIAL. LACM 151244, a fragment from the proximal part of a right scapula collected in 1966 from locality LACM 6688.

DISCUSSION. This right scapula fragment has a depression in the bone on the outer margin of the glenoid fossa at the location where the coracoid process meets the glenoid fossa. There are also osteophytes encircling the outer rim of the glenoid fossa. There is a second depression in the bone on the lateral margin of the glenoid fossa. The surface of the glenoid fossa is rough and pitted as would be present in a case of spondyloarthropathy.

Pathologic Humerus

MATERIAL. LACM 7008, a left humerus collected by Dan Shellhammer at locality LACM 1655.

DISCUSSION. This mysticete left humerus has an idiopathic lesion on the posteromedial margin of the distal part of the diaphysis. The lesion is a raised bump of bone that is approximately 35 by 30 mm in diameter at its base, and Aufderheide and Rodríguez-Martín (1998:fig. 9.6) show a similar-appearing lesion. Trauma cannot be excluded as the cause of this lesion.

Pathologic Radius

MATERIAL. LACM 6443, a right radius collected by Richard C. Bishop in 1963 at locality LACM 1625.

DISCUSSION. This radius has osteophytes around the articular facets for the humerus and ulna, as well as an incompletely fused distal epiphysis (Fig. 4J), and the epiphysis is also somewhat eroded.

Pathologic Phalanges

MATERIAL. Phalanges: LACM 45224 and LACM 63819, both collected by Edward D. Mitchell, Jr., and Camm C. Swift in 1963 at locality LACM 1625; phalanx: LACM 119454, collected by William Hawes, Jr., in December 1975 at locality LACM 3160.

DISCUSSION. LACM 45224 has hyperostotic lipping around the distal articular surface and bone resorption as well as extra bone growth on the lateral most margin of the proximal articular surface. The proximal articular surface has a series of connected pits starting near the dorsal midpoint of the phalanx and progressing to the lateral edge. On the lateral side of the phalanx is a raised bump of bone projecting posterolaterally. The surface of this bump is composed of reactive new bone, indicating relatively rapid development. LACM 63819 has hyperostotic lipping at the site of fusion of the two phalanges. The fusion of these two phalanges does not appear to be trauma induced. LACM 119454 has two idiopathic bony growths (see similar structures in Aufderheide and Rodríguez-Martín, 1998 and Rothschild and Martin, 1993) on its distal articular surface. This phalanx also has hyperostotic lipping around its distal articular surface.

Suborder Odontoceti (Flower, 1865) Flower, 1867

COMMENTS

Nine species of extinct dolphinlike odontocete cetaceans were named from the Sharktooth Hill Bonebed by Kellogg (1931) based on isolated petrosal bones. Kellogg assigned most of these to the family Delphinidae, but such family assignments were commonly made at that time for many small fossil dolphinlike odontocetes. Without associated crania and skeletons, however, such family assignments are conjectural for taxa that are based on isolated petrosals. The true identities of most of Kellogg's small odontocete taxa remain problematic.

To date, the identities of only four of Kellogg's named odontocetes have been learned. Barnes and Mitchell (1984) concluded that *Grypolithax obscura* Kellogg, 1931, is a small kentriodontine kentriodontid delphinoid belonging to the genus *Kentriodon* Kellogg, 1927a, and that *Grypolithax pavida* Kellogg, 1931, is its junior synonym. Barnes et al. (2005) noted that most of the other small odontocetes in the assemblage are kentriodontid dolphins. Flores-Trujillo et al. (2000) determined on the basis of a middle Miocene cranium and associated petrosal from Baja California that *Liolithax kernensis* Kellogg, 1931, is a kentriodontine that has a longer snout than any species of *Kentriodon*. Barnes (1977, 2006) determined that *"Squalodon" errabundus* Kellogg,

1931, is a platanistoid dolphin based on two occurrences of petrosals found directly associated with crania, but the postcranial osteology of this species is not yet known. *Aulophyseter morricei* Kellogg, 1927b, is the most abundant sperm whale in the Sharktooth Hill Local Fauna (Barnes, 1977; Barnes et al., 2005; Kimura et al., 2006), but a few larger sperm whale teeth from the bonebed that have crenulated enamel on their crowns would traditionally be identified as *Scaldicetus* (Hirota and Barnes, 1995; Kimura et al., 2006).

Family Physeteridae Gray, 1821

Aulophyseter morricei Kellogg, 1927b

MATERIAL. LACM 21184, right humerus collected by Edward D. Mitchell, Jr., in October 1960 at locality LACM 1557; LACM 21194, left radius collected by Edward D. Mitchell, Jr., in October 1960 at locality LACM 1557; LACM 21247, right humerus collected by Joseph F. Arndt prior to 1960 at locality LACM 1556; LACM 50825, right radius collected by William Hawes, Jr., 16 March 1973 at locality LACM 3160; LACM 74061, left radius collected by William Hawes, Jr., in February to April 1973 at locality LACM 3160; LACM 103398, proximal left ulna collected by Paul Kirkland and Roberta Kirkland on 14 February 1976 at locality LACM 1622; LACM 127712, right humerus collected by Howell W. Thomas in 1979 at locality LACM 3162; LACM 151243, fused radius, ulna, and proximal carpal bone collected by Howell W. Thomas in 1979 at locality LACM 3162.

DISCUSSION. These humeri were referred to *Aulophyseter morricei* by Kimura et al. (2006:fig. 8a–c). In addition to these humeri, we also refer to *A. morricei* the radii and ulnae that are listed here because they are from relatively small physeterids, they articulate appropriately with the humeri that we refer to this species, and they resemble the homologous bones of the primitive middle Miocene sperm whale *Brygmophyseter shigensis* (Hirota and Barnes, 1995) (and see Kimura et al., 2006) from Japan. The humeri of *A. morricei* from the Sharktooth Hill Bonebed (Fig. 4B and 4E) are smaller and more slender than the humerus of *B. shigensis* (see Hirota and Barnes, 1995:fig. 15), and they resemble other sperm whale humeri by having a relatively short and stout diaphysis, an elongate and prominent deltopectoral crest that incorporates a prominent anteriorly directed tubercle, and an obliquely canted distal trochlea for the ulna that is not divided into two facets. The series of humeri reported here (Fig. 4A–4F) show progressive size increase correlated with maturity, as well as some individual variation.

The right humerus, LACM 21184, has osteophytes around the capitulum for the radius and the trochlea for the ulna, as well as rugose bone growth along the lateral margin of the deltopectoral crest (Fig. 4A and 4D). A second right humerus, LACM 127712 (Fig. 4B and 4E), has an osteoid osteoma, which is a buttonlike bone tumor of idiopathic origin, on its posteromedial margin about half way along the diaphysis (Fig. 4E-1, and for another example see Zimmerman and Kelley, 1982). Also on this humerus are osteophytes around the capitulum for the radius and the trochlea for the ulna and a rugose bone growth distal to the deltopectoral crest. Although we are not addressing predation in this paper, this specimen is of additional interest because broken portions of three shark teeth are imbedded in it. The pathologies noted here could not have been a result of sharks biting the animal; there is no healing present at the sites of the shark bites, and the pathologies that we note would have taken considerable time to develop.

Another right humerus, LACM 21247, that we refer to *A. morricei* has osteophytes around the articular facets for the radius and ulna and rugose bone growth distal to the deltopectoral crest extending caudally along the medial margin of the crest and terminating at the proximal medial edge of the deltopectoral crest (Fig. 4C and 4F).

The fused radius and ulna (LACM 151243, and an attached proximal carpal) that we refer to *A. morricei* resemble those of *B. shigensis* (see Hirota and Barnes, 1995:fig. 15) by being expanded distally, wide anteroposteriorly, and flattened transversely, but they differ from the same bones of *B. shigensis* by being shorter proximodistally. The radius of *A. morricei* is typical of sperm whales by having an obliquely positioned proximal facet for articulation with the humerus and a relatively large ulnar facet. The ulna that is fused to this radius is typical of sperm whales (see Van Bénéden and Gervais, 1868–1880:pl. XVIII) by having a single articular surface for articulation with the humerus and a large, broad, and posteriorly projecting olecranon process. The other radii (LACM 21194, 50825, and 74061), and the ulna (LACM 103398) that we also refer to *A. morricei* resemble the same bones of LACM 151243.

The radius of LACM 151243 is pathologically fused to the proximal carpal bone (Fig. 4G-1), with which the radius and ulna both normally articulate and to which in life they would have been joined by fibro-cartilage. In the normal condition, all three bones would have been separate. Osteophytes are around the proximal articular facets of both the radius and the ulna (Fig. 4G-2 and 4H-1), and the ulna has osteophytes on the distal lateral portion of its olecranon process. The distal end of the ulna has a portion of the epiphysis fused to it, and the remainder of the epiphysis was broken off and is missing (see Fig. 4G-3). Where, in a normal whale, the proximal ends of the radius and ulna would have been in contact there is instead a separation of approximately 15 mm. This separation indicates that to

have articulated with both the radius and the ulna, the distal articular facets of the corresponding humerus would have been abnormally wide anteroposteriorly. The radius and ulna both have deep lacerations from shark teeth, as do another radius, LACM 74061 (Fig. 7B), and another ulna, LACM 103398. The radius, LACM 21194, has in addition to osteophytes around the humeral and ulnar facets an incompletely fused distal epiphysis, and the epiphysis is also somewhat eroded. The partial ulna, LACM 103398, has osteophytes around its humeral and radial facets.

Physeteridae

Genus and Species Undetermined

MATERIAL. LACM 74077, right humerus collected by Lawrence G. Barnes on 7 April 1973 at locality LACM 3160.

DISCUSSION. This humerus is typical of sperm whales by being short and stout, having a long deltopectoral crest, and having an inclined trochlea for the ulna that only has one plane, rather than the two separate facets that usually exist in most Cetacea. It is the only example of this type of humerus that we have observed in all of the collections from the Sharktooth Hill Bonebed. All of the other physeterid humeri are suitably similar to one another, relatively abundant, and can be confidently referred to *A. morricei* (as noted in previous section under *Aulophyseter morricei*, and see Kimura et al., 2006).

In addition to the more common sperm whale, *A. morricei*, there is another much more rare sperm whale in the Sharktooth Hill Local Fauna, and its presence has been indicated by teeth that have a thick crenulated enamel cap that are typically referred to the form genus *Scaldicetus* (*sensu* Kimura et al., 2006). The humerus, LACM 74077, might represent the sperm whale that had such teeth. The distal part of this humerus has osteophytes around the articular facets for the radius and ulna. There is a bony ridge around the facet for the olecranon process of the ulna, and the surface of the facet is rough and pitted (Fig. 4I-1). A small bony bump on the medial side of this facet measures 9 by 8 mm in circumference and approximately 3 mm high at its apex (Fig. 4I-2).

Superfamily Delphinoidea (Gray, 1821) Flower, 1865

?Family Kentriodontidae (Slijper, 1936) Barnes, 1979

Genus and Species Undetermined, large species

MATERIAL. LACM 151219, axis vertebra collected by Howell W. Thomas in 1979 at locality LACM 3162.

DISCUSSION. This specimen, previously reported by Thomas and Barnes (2002), is the axis (second cervical) vertebra belonging to a large dolphinlike odontocete, possibly a kentriodontid, whose precise identity is presently unknown. It measures 134 mm in maximum width across the transverse processes and 92 mm across the anterior articular facets, and the maximum width of the neural canal is 29 mm.

This axis vertebra appears to belong to some species of kentriodontid because it shares with the axis (see Dawson, 1996:fig. 7) of the similarly large lophocetine kentriodontid *Hadrodelphis calvertense* from the Calvert Formation of Maryland large, oval-shaped anterior articular facets, a large odontoid process, a triangular-shaped neural canal, and elongate ventrolaterally directed transverse processes. The only large dolphinlike odontocete among those that Kellogg (1931) named on the basis of petrosals is *Platylithax robusta* Kellogg, 1931. No additional specimens have been referred to this species, and its true identity remains a mystery. Although there is no way at the present time to precisely identify the pathologic axis vertebra, LACM 151219 is possibly from a large kentriodontid.

This axis exhibits idiopathic breakage of its posterior vertebral epiphysis and subsequent healing. It also has extensive osteophytosis in the area of this injury. Hyperostotic lipping along the entire ventral edge of the posterior section of the vertebra and continues slightly more than half-way along the left edge. The lipping is most well developed along the left ventrolateral side of the centrum (Fig. 5I-1). There is a bony projection on the ventral side of the right transverse process (Fig. 5J-1).

The posterior epiphysis has been broken into four distinct sections, and each of these broken sections has been forced ventrally (Fig. 5I-2). The broken sections remained fused to the vertebra. This leads to the conclusion that this breakage must have happened over an extended period of time, rather than during a one-time traumatic event. One possible explanation for the breakage could be that some object, possibly a bony growth, was interposed in the cartilage between this axis vertebra and the adjacent third cervical vertebra. Alternatively, it is possible that the damage to this vertebra could have been caused by something on the third cervical vertebra that was continuously hitting this area of the axis vertebra during the undulating motions in the body of this dolphin while it was swimming.

The behavior of living delphinid odontocetes might provide another possible cause for the major bone fracture on this vertebra. Living delphinids are known to be combative with other predators, such as sharks. Dolphins are known to ram sharks with their beaks. Such a behavior, in the case of the fossil from the Sharktooth Hill Bonebed, could have produced an impact suffi-

cient to damage a section of this vertebra. Alternatively, a less dramatic source of such injury might have been simply accidentally swimming head-on into an obstacle. However, considering the known echolocating abilities of odontocetes, this is probably a less likely cause than the first suggestion. Another possibility is that the cartilage between the axis vertebra and the third cervical vertebra was damaged or diseased or that the third cervical vertebra had a growth on it that affected the axis vertebra over a long period of time.

MATERIAL. LACM 53928, right humerus collected by Ruth Dillon and Claire Dillon in 1974 at locality LACM 1622.

DISCUSSION. This humerus is from a large delphinoid odontocete, possibly a kentriodontid, and it might belong to the same large species as the prior specimen. The humerus has osteophytes around the articular surfaces for the radius and ulna and a myositis ossificans scar (see Zimmerman and Kelley, 1982:fig. 32). A ridge of bone has developed along the lateral edge of the facet for the olecranon process of the ulna. The surface of the facet is sloped from a high point on the lateral side to a lower level on the medial side, where there is no ridge of bone. The surface of the facet is pitted and rough. The humeral head has an abnormal triangular depression on its lateral edge. The surface of this depression is smooth bone, indicating that the depression developed over time and that the surface continued to reheal even as the depression progressively deepened. There is a small area of hyperostotic lipping on the proximal edge of the humeral head.

?Family Kentriodontidae (Slijper, 1936) Barnes, 1979

Various Undetermined, small species

MATERIAL. Vertebrae: LACM 98789, cervical vertebra collected by Paul Kirkland and Roberta Kirkland in 1975 at locality LACM 1625; LACM 115127, associated atlas and axis vertebrae collected by William A. Walker in 1967 at locality LACM 6688; LACM 151231, axis vertebra collected by Michael D. Quarles in 1973 at locality LACM 3162; LACM 151232, lumbar vertebra collected by Raj B. Naidu at locality LACM 3160; LACM 151236, atlas vertebra, LACM 151237, thoracic vertebra, LACM 151238, anterior caudal vertebra, LACM 151239, posterior caudal vertebra all collected by Howell W. Thomas in 1979 at locality LACM 3162; LACM 151250, axis vertebra from locality LACM 6688.

DISCUSSION. A cervical vertebra, LACM 98789, has anteroposterior expansion of the ventral portion of the centrum (Fig. 8A and 8B). LACM 115127, associated atlas and axis vertebrae, both have pathologies. The atlas has a fold on the medial margin of the left articular facet for the occipital condyle of the cranium (Fig. 8C-1). The posterior facets for the axis vertebra are asymmetrical, with the right facet extending farther laterally than the left (Fig. 8D-1). There is hyperostotic lipping around the entire margin of the right posterior articular facet and on the dorsal and lateral margins of the left posterior articular facet (Fig. 8D). The axis vertebra shows hyperostosis on the ventral side of the dorsal process (Fig. 8E-1), as well as on the posterior surface of the dorsal process (Fig. 8E-2). There are bony projections formed on the ventral surface of the vertebra immediately ventral to and posterior to both articular facets for the atlas vertebra (Fig. 8E-3). Both transverse processes of the axis vertebra have bony projections that had grown around the posterodorsal margin.

LACM 151231 is an axis vertebra that has rough bone surface with some resorption of bone tissue (Fig. 8G). LACM 151232 is a lumbar vertebra that has on the right side of the posterior part of the centrum extreme osteophytic growth (marginal syndesmophytes), and this growth overlapped the centrum of the adjacent vertebra anterior to it (Fig. 8H and 8I). There is one smaller osteophyte on the right posteroventral margin of this vertebra. On the posteroventral edge of the centrum is rough bone, indicating that perhaps the next vertebra had anterior osteophytic growth overlapping this vertebra. These osteophytic growths are consistent with spondyloarthropathy (see Rothschild and Martin, 1993:101–116). An atlas vertebra, LACM 151236, has a fold in the medial margin of the left articular facet for the occipital condyle of the cranium (Fig. 8J), as well as hyperostotic lipping around both articular facets for the axis vertebra (Fig. 8K).

LACM 151237 is a thoracic vertebra that has evidence of a *Brucellosis*-type bacterial infection that affected the anterior part of the vertebral centrum with pitting and resorption of the centrum (Fig. 8L). The ventral surface of the centrum has striated bone growths that extend the full length of the vertebra (Fig. 8M) and end in hyperostotic bone growths along the posteroventral margin of the vertebra (Fig. 8N-1). The posterior part of the centrum has pitting and erosion of the surface (Fig. 8N-2) of the bone in the middle of the centrum and epiphyseal ring fragmentation that is consistent with a Schmorl's node (see Roberts and Manchester, 1995).

LACM 151238 is an anterior caudal vertebra with hyperostotic bone growth on the right posteroventral part of its centrum (Fig. 8O–8R). It also has asymmetrical development of the transverse foramen; the foramen never formed on the left side of the vertebra. LACM 151239 is

a more posterior caudal vertebra that has a line of hyperostotic bone growth extending across the middle of the left pedicle of its dorsal process (Fig. 8S-1). There is also a line of hyperostotic bone growth on both sides near the base of its dorsal process (Fig. 8S-2 and 8T-1). LACM 151250 is an axis vertebra that has bony overgrowths on the medial margins of both articular facets for the atlas vertebra. The growths are each approximately 10 mm long, 3 mm wide, and 1 mm high at their highest points. A sharp ridge on the anterior edge of the bony growth flares smoothly into the vertebral pedicle. Also, hyperostotic lipping is around the ventral edges of the dens where it articulates with the atlas vertebra.

MATERIAL. Humeri: LACM 50822, right humerus collected by William Hawes, Jr., in 1973 at locality LACM 3160; LACM 51078, left humerus collected by Joseph F. Arndt in 1966 at locality LACM 6688; LACM 78853 and LACM 78854, left humeri collected by Lawrence G. Barnes and Michael D. Quarles in 1973 at locality LACM 3160; LACM 98714, right humerus collected by Paul Kirkland and Roberta Kirkland in 1976 at locality LACM 3160; LACM 151220, left humerus collected by Howell W. Thomas in 1979 at locality LACM 3162; LACM 151233, right humerus collected by Raj B. Naidu at locality LACM 3160; LACM 151234 and LACM 151235, two humeri collected by William Hawes, Jr., in 1979 at locality LACM 3162; LACM 151240, right humerus collected by Howell W. Thomas in 1979 at locality LACM 3162; LACM 151246, right humerus collected by Paul Kirkland and Roberta Kirkland in 1973 at locality LACM 1655; LACM 151248, right humerus collected by Joseph F. Arndt in 1966 at locality LACM 6688.

DISCUSSION. LACM 151220 is the humerus of a small dolphinlike odontocete, possibly a kentriodontid, but its precise identity is presently unknown. It resembles the larger humerus of *H. calvertense*, from which it differs by having a relatively smaller head and more gracile apophysis. It might belong to a small kentriodontid approximately the size of *Kentriodon obscurus* (Kellogg, 1931) or to any of the other small kentriodontids in the Sharktooth Hill Local Fauna. This humerus has a myositis ossificans traumatica (see Zimmerman and Kelley, 1982) scar on the posterior side of the diaphysis. This humerus also has pathology around the trochlea that articulated with the ulna. In life, the olecranon process of the ulna was fused to the distal end of the humerus. The fusion is around the posterior perimeter of the trochlea of the humerus, where an exostosis had grown around the apex of the olecranon process. After death, the two bones broke apart, and the apex of the olecranon process remained attached to the humerus (Fig. 6A). This pathology is very similar to that which is described in the following text for the humerus and ulna of the latest Miocene phocoenid porpoise, *Piscolithax tedfordi* Barnes, 1984, from Mexico.

Ten other humeri of small odontocetes, most of them probably belonging to kentriodontid dolphins, show similar pathologies, but to a lesser extent. Each of these has a myositis scar, and each one has bone deformation at the humeral–ulnar articulation. None of these 10, however, had become fused at the humeral–ulnar joint. In addition to having the myositis scar and bone deformation at the humeral–ulnar articulation, humeri LACM 51078 and LACM 151240 both have rugose bone growths along the ventral margin of the deltopectoral crest, and these bone growths extend around the base of the deltopectoral crest both anteriorly and posteriorly. Anteriorly, the bone growths progress medially along the anteromedial rim of the greater tuberosity (Fig. 6B). Additionally, the humerus LACM 151240 has rugose bone growth surrounding the infraspinatus fossa, and it also has a small bony growth on the lateral margin of the posterior part of the deltopectoral crest (Fig. 6C) that is similar in appearance to a button osteoma.

LACM 151246, an odontocete right humerus, has an idiopathic ovoid depression measuring 11 by 7 mm on its posterolateral margin distal to the humeral head (Fig. 6D). LACM 21184, another odontocete right humerus, has osteophytes around the articular facets for the radius and ulna, as well as rugose bone growth along the lateral margin of the deltopectoral crest.

MATERIAL. Radii: LACM 45339, right radius collected by Camm C. Swift and Edward D. Mitchell, Jr., in 1963 at locality LACM 1625; LACM 50825 and LACM 74061, right radii collected by William Hawes, Jr., in 1973 at locality LACM 3160.

DISCUSSION. These three radii all have osteophytes around their humeral and proximal ulnar articulations. LACM 45339 has osteophytes around the proximal trochlea, as well as hyperostotic lipping around its distal articular facets (Fig. 7A).

MATERIAL. Ulnae: LACM 41468, left ulna collected at locality LACM 1655; LACM 50634, right ulna collected by LACM field party in 1966 at locality LACM 6688; LACM 119485, right ulna collected by William Hawes, Jr., at locality LACM 3499; LACM 151242, right ulna collected by Howell W. Thomas in 1979 at locality LACM 3162.

DISCUSSION. The left ulna LACM 41468 has osteophytes around the humeral and the proximal radial facets. Hyperostotic lipping around the edges enlarged its radial facet. The normally smooth surface of the articular facet has, in this

specimen, been eroded to produce a pitted and roughened surface (Fig. 7C). A right ulna, LACM 50634, has osteophytes as well as hyperostotic lipping around all of its articular surfaces (Fig. 7D–7G). A bony bump at the proximal edge of the radial facet is approximately 8 mm wide and projects approximately 1 mm above the surface of the radial facet (Fig. 7G-1). Ulnae LACM 119485 and LACM 151242 both have osteophytes around their humeral and radial articulations, as well as bone deformation of their proximal humeral facets (Fig. 7H–7M). LACM 119485 has a bony bump on the proximal radial facet that measures 5 by 4 mm and is 2 mm high (Fig. 7H-1 and 7J-1). The radial articulation of LACM 151242 has a roughened surface with some pitting (Fig. 7M).

EXAMPLE FROM THE LATE MIOCENE MONTEREY FORMATION

Geology and Age

Strata referred to the late Miocene Monterey Formation in Orange County, California, are deep-water sediments that have been correlated with the Margaritan provisional provincial age of Addicott (1972), the Clarendonian North American Land Mammal Age, and the Mohnian and Delmontian foraminiferal stages (Barnes, 1977:328, 330, 1978; Domning, 1978). Several fossil marine vertebrate assemblages have been reported from different horizons in this rock unit (Barnes, 1977:330; Domning, 1978; Barnes et al., 1985).

Suborder Odontoceti (Flower, 1865) Flower, 1867

Superfamily Delphinoidea (Gray, 1821) Flower, 1865

Genus and Species Undetermined

MATERIAL. LACM 151245, right humerus from locality LACM 7431.

DISCUSSION. This specimen was first reported by Thomas and Barnes (2002). Barnes (1977:330) reported several small odontocetes from the Monterey Formation in southern Orange County, but only one of these has been identified at the species level: the pithanodelphinine kentriodontid *Atocetus nasalis* (Barnes, 1985). We conclude that the humerus under consideration here does not represent *A. nasalis* because, although the humerus of this species is not known, LACM 151245 is smaller and more gracile than the humerus that is part of the holotypic skeleton of a closely related late Miocene species from Peru called *Atocetus iquensis* Muizon, 1988.

This humerus from California exhibits myositis ossificans traumatica (Fig. 6E-1), which might have resulted from a torn ligament in the proximal part of its foreflipper. Along the distal posterior side of the diaphysis of the humerus there is a somewhat rectangular-shaped bony growth that measures approximately 9 by 4 mm. This growth is consistent with the occurrence of a torn ligament because osteophytes form while new bone continues to grow at the original site of ligament attachment.

EXAMPLES FROM THE LATEST MIOCENE ALMEJAS FORMATION

Geology and Age

Fossil marine vertebrates are found near the southeast corner of Isla Cedros in the Lower Member of the Almejas Formation, and are of latest Miocene age, approximately 6 to 8 Ma. Repenning and Tedford (1977) and Barnes (1984:fig. 1, 1992) have discussed the age of the fossil vertebrate–bearing Lower Member of the Almejas Formation and have concluded that it is correlative with the Jacalitos and/or Etchegoin provisional provincial marine invertebrate stages of Addicott (1972).

Invertebrate fossils that aid in geochronology are found only in the Upper Member of the Almejas Formation from sediments that are stratigraphically above the vertebrate-bearing horizons in the Lower Member of the formation, and these invertebrates are correlative with those from the San Diego Formation, of late Pliocene age in Southern California (Repenning and Tedford, 1977). The marine vertebrate assemblage in the Lower Member of the formation is correlative with those from the lower parts of the Purisima and Capistrano formations in California, both of which are latest Miocene age, and from parts of the Pisco Formation in Peru (Barnes, 1977, 1984, 1992; Repenning and Tedford, 1977).

The holotypic skeleton of the primitive phocoenid porpoise *Piscolithax tedfordi* (see the Family Phocoenidae section for discussion), was collected in Unit 6 of the Lower Member of the Almejas Formation, specifically 15 feet (4.6 m) stratigraphically above the conglomeratic base of the Lower Member, which also is the lowest bed in the formation. The holotypic skeleton of the albireonid delphinoid odontocete *Albireo whistleri* Barnes, 1984, was discovered at approximately the same level as the holotype of *P. tedfordi* within the Lower Member of the formation.

Suborder Odontoceti (Flower, 1865) Flower, 1867

Family Albireonidae Barnes, 1984

Albireo whistleri Barnes, 1984

MATERIAL. UCMP 314589 (formerly UCR 14589), a nearly complete skeleton including the cranium, both petrosals, both tympanic bullae, auditory ossicles, mandible with teeth in place, isolated teeth, and nearly complete postcranial skeleton, lacking only the posterior lumbar vertebrae and all of the caudal vertebrae, collected by David P. Whistler and George T. Jefferson on 15 July 1964 at UCR locality RV-7309, southeastern Isla Cedros, Baja California, Mexico.

DISCUSSION. The morphology of the strange odontocete *Albireo whistleri* is well known (e.g., Barnes, 1992, 2006, 2008; Fordyce and Barnes, 1994) by its nearly complete holotypic skeleton from Isla Cedros. It was discovered in the Lower Member of the Almejas Formation, at approximately the same stratigraphic level within the formation (see Barnes, 1984) as was the holotype of *P. tedfordi*, discussed below. The complete osteology of this specimen is described elsewhere (Barnes, 2008).

The skeleton has a possible pathology; the posterior articular surfaces of the atlas vertebra of the holotype (see Barnes, 2008:fig. 22b) are asymmetrical both in size and shape. The right posterior articular surface has a uniformly crescentic outline, as would be expected on this bone in a cetacean. The left articular surface, however, extends laterally onto the base of the transverse process. The opposite is the case on the holotypic atlas of *Albireo savagei* Barnes, 2008: Its right articular surface extends laterally onto the base of its transverse process. This asymmetry might have been caused by illness or injury, or alternatively, it might have been caused by "handedness," wherein the individual turned more frequently to one side than the other.

Family Phocoenidae (Gray, 1825) Bravard, 1884

Piscolithax tedfordi Barnes, 1984

MATERIAL. UCMP 315972 (formerly UCR 15972); the holotypic partial skeleton, including the partly restored cranium, right and left tympanic bullae and petrosals, right and left stapes, right incus, posterior ends of both dentaries, hyoid bones, vertebrae, ribs, both humeri, both radii, right ulna, and possible sternal rib. The skeleton was collected in two phases: the first by David P. Whistler and Richard H. Tedford, on 6 August 1965 and the second by David P. Whistler, Francisco J. Aranda-Manteca, Lawrence G. Barnes, and Thomas A. Deméré, on 12 March 1992. The specimen was collected at UCR locality RV-6505 (Field Locality 11), in "Arroyo Esqueletos," in the southeastern part of Isla Cedros, Baja California, Mexico.

DISCUSSION. The cranium, parts of the mandible, petrosals, bullae, both humeri, and the left radius were the first parts of the holotypic skeleton to be collected, with the field number R.H. Tedford 1278. Much of the remainder of the skeleton, collected with the field number L.G. Barnes 3392, was removed in its associated condition within the enclosing sediment in one plaster and burlap jacket. The positions of the bones in this second part of the skeleton were recorded in the laboratory as they were removed. In addition to the similarity in size and preservation of the bones collected on the two different dates, the discovery of the right ulna among the bones collected in 1992 demonstrates unquestionably that the two parts of the skeleton, collected 27 years apart, are from the same individual.

The pathology of the right forelimb bones of this specimen proves conclusively that all bones belong to the same individual. The right elbow joint, unlike the left, was in life fused because of excessive osteosclerotic overgrowth of the joint margins (Fig. 9A). During fossilization and sediment compaction, the fused right humerus and ulna were broken apart and became separated. The right humerus, which was collected on 6 August 1965, fits perfectly onto the right ulna, which was collected on 12 March 1992; the broken point of fusion joins perfectly, with no missing bone. The left ulna of this specimen has not been recovered. Fortuitously, if the unfused left ulna had been found rather than the fused right ulna, it could not have been proven that the parts that were collected 27 years apart belong to the same individual.

Both right and left humeri were collected in 1965 when the specimen was first found. Both humeri have extreme spur formation around the trochlea for the ulnae. On the right humerus, this resulted in the aforementioned pathologic fusion of the humerus and ulna. The two humeri are not identical, each being modified to a different extent by osteoarthritis (a similar case was reported by Rothschild and Martin, 1993:81–87). Exostoses are present on both humeri around the posterior borders of the trochlea for the ulna (Fig. 9B and 9C). The right humerus, which has the more extensive development of the osteoarthritis, has a thicker diaphysis and is more expanded distally than is the less modified left humerus. Because of this, the less modified left humerus is the best representation of this bone for the species (Fig. 9D and 9F). Both humeri of *Piscolithax tedfordi* have unusually rugose surfaces, undoubtedly attributable both to extreme maturity as well as to the osteoarthritic condition. Both humeri also exhibit osteoarthritic lipping around margins of the humeral heads (Fig. 9C and 9D). The left humerus has an idiopathic groove in the humeral head (Fig. 9E) and a bony spur extending caudally from the lateral edge of the greater trochanter (Fig. 9F).

In the unmodified state, the infraspinous fossa is very deep, elongate proximodistally, and positioned near the anterior border of the body of the bone. The right humerus is modified by the osteoarthritic condition by having, in addition to the bone spur around the joint that fused to the ulna, a more rugose surface, a wider distal part of the body, and a smaller infraspinous fossa that is partly filled with an irregular mass of bone (Fig. 9C). The grooving of the distal articular surfaces is probably also related to the osteoarthritis (see Rothschild and Martin, 1993:82).

Both radii are preserved with the holotype: the left (Fig. 9G–9I) collected in 1965 and the right collected in 1992. Of the two, the right radius is the more complete, but both are badly cracked. The right radius is slightly more expanded anteroposteriorly than the left, measuring approximately 8 mm wider in the distal half of the body of the bone, and this may be related to the osteoarthritic condition of the right forelimb. The right radius has osteoarthritic lipping around the proximal ulnar facet, and bone resorption occurred within this facet. This radius also has osteophytes around the distal trochleae for the carpal bones. The left radius has osteophytes around the proximal trochleae for the humerus and ulna (Fig. 9I). The true shape of the olecranon process of the ulna is somewhat obliterated, and its size is slightly enhanced by the osteophyte (Fig. 9J and 9K) from the osteoarthritis that had formed the spurs fusing the ulna and the humerus.

The damage to the foreflippers of the holotype of *P. tedfordi* may be the result of a possible metabolic osteoarthritis. At the time of death, its disease was sufficiently advanced to cause the right humerus and ulna to become fused together. This probably did not negatively affect its swimming abilities because the elbow joints of all modern Cetacea, while not normally fused, are structurally rigid.

EXAMPLE FROM THE LATE PLIOCENE PISMO FORMATION

Geology and Age

This specimen was collected in a road cut, approximately 1 m above the road grade, across the road from the Union Oil Company pier, on the north side of the road that goes from Avila Beach to Port San Luis, Avila Beach, San Luis Obispo County, California.

The rock unit exposed here is the Squire Member of the Pismo Formation, which is late Pliocene in age, approximately 3 to 2 Ma, and correlative with the Blancan North American Land Mammal Age (see Hall, 1973; Domning, 1978:75, 160). The stratum that contained the holotypic skeleton of *Albireo savagei* is a coarse-grained, yellowish-colored, firm, nonindurated sandstone that contains rounded cobbles. Stratigraphically above this horizon is a white sandstone. Stratigraphically below the level of the holotype of *A. savagei*, the yellow sandstone contains angular rock clasts, and this grades downward into greenish sandstone that disconformably overlies volcanic rocks.

The type locality of *A. savagei* and nearby localities have produced a small but important assemblage of fossil marine vertebrates and invertebrates: the pectinid *Lyropecten cerrosensis* (Gabb, 1866), an extinct grebe *Gavia* cf. *G. concinna* (Wetmore, 1940), an otariine pinniped, a balaenopterid mysticete whale, a horse identified as *Equus* sp., and the primitive relative of Steller's Sea Cow, *Hydrodamalis cuestae* Domning, 1978. The holotype (UCMP 86433) of *H. cuestae* was found at the same locality as the holotype of *A. savagei*, but from slightly higher stratigraphically in the section.

Suborder Odontoceti (Flower, 1865) Flower, 1867

Family Albireonidae Barnes, 1984

Albireo Barnes, 1984

Albireo savagei Barnes, 2008

MATERIAL. UCMP 112048, the partial holotypic skeleton of one individual, including atlas vertebra, thoracic vertebrae numbers 4, 5, 6, 7, 8, and possibly 11, and parts of several ribs, collected by Donald E. Savage and Lawrence G. Barnes on 17 and 18 September 1970 at locality UCMP V-70148, L.G. Barnes field number 590.

DISCUSSION. This relatively derived species of *Albireo* is named elsewhere in this volume (Barnes, 2008) on the basis of a partial skeleton. Its atlas vertebra (see Barnes, 2008:fig. 22) is equally as completely preserved as that from the holotypic skeleton of *A. whistleri* from Isla Cedros, and like that atlas, it is also asymmetrical. Its asymmetry involves the posterior articular surfaces, which are asymmetrical both in size and shape. The left posterior articular surface has a uniform crescentic outline, but the right articular surface extends laterally onto the base of the transverse process. The opposite is the case on the holotypic atlas of *A. whistleri*: Its left articular surface extends laterally onto the base of the transverse process. The presence of these same asymmetries in both known specimens of *Albireo* suggests a tendency for the development of pathologies in the atlas and axis vertebrae of these dolphins.

CONCLUSIONS

1. Bone pathologies are easily preserved in the fossil record, and they are the primary

evidence of disease and injury in fossil mammal specimens. The study of paleopathology, although relatively extensive, has not been uniform among the various mammal groups. Bone pathologies occur relatively frequently among Recent marine mammals, and they are also present in fossil marine mammals.

2. Specimens of fossil Cetacea from various localities worldwide exhibit damage and modifications to bones resulting from pathology. Cetacean pathologies have been described in some taxonomic or descriptive studies, involve members of the Archaeoceti, Mysticeti, and Odontoceti, and occur as early as the late Eocene. Usually the reason for the pathology was not determined or suggested.
3. Some new examples of cetacean pathologies have been discovered from fossil deposits in western North America. These range in age from late Oligocene to late Pliocene, and they affected members of the Mysticeti and Odontoceti. Some of these examples are single-specimen occurrences, and others are from a mass accumulation, the middle Miocene Sharktooth Hill Bonebed in central California. Some specimens cannot be identified beyond the subordinal level, but others are parts of holotypes of named species.
4. The cetacean pathologies include fractures (most of which were healed), idiopathic growths (bony growths of unknown cause), osteophytoses (masses of bony growth similar in appearance to, although larger than, osteoid osteomas [which are buttonlike bony growths]), hyperostoses (excess bony growth, including hyperostotic lipping), resorptive bone degeneration of idiopathic origin, a possible example of a Schmorl's node (a small depression in a vertebral centrum), possible metabolic osteoarthritis, myositis ossificans traumatica scars (apparently resulting from torn ligaments), *Brucellosis*-like bacterial infections, abnormal fusions between bones, and possible congenital asymmetry. These pathologies affected vertebrae, ribs, and forelimb bones—among the latter, particularly at the elbow joint.
5. One of the geochronologically earliest examples of a fossil cetacean pathology is two pathologic thoracic vertebrae of an unidentified midsize mysticete from the late Oligocene Pysht Formation on the Olympic Peninsula, Washington state.
6. Large collections from the middle Miocene age Sharktooth Hill Bonebed in Kern County, central California, provided the majority of the examples that are documented here. Affected cetaceans in the assemblage include mysticetes, various small odontocetes, and sperm whales.
7. In one case, bone pathology provided forensic evidence for the association of disparate parts of the holotype of the primitive phocoenid porpoise, *Piscolithax tedfordi*. This important skeleton is from the latest Miocene age Lower Member of the Almejas Formation on Isla Cedros, Baja California, Mexico. The humerus was collected with the anterior part of the holotypic skeleton in 1965, and the ulna was collected with the posterior part of the skeleton in 1992. In life, the humerus and ulna had become pathologically fused, but they subsequently broke and became separated during fossilization. The pathology provided unquestionable evidence that the two parts of the holotypic skeleton, collected 27 years apart, belong to one individual.
8. No evidence was detected in any of the specimens of avascular necrosis, a condition resulting from "the bends." This pathology has been previously reported in various fossil whales of Oligocene to Pliocene age, and in Recent whales.
9. It is important to note that each of the examples reported here is from an individual that appears to have survived with its ailment for a considerable period of time, even a dolphin that had an extremely pathologic axis vertebral epiphysis that might have affected its spinal cord. Pathologies similar to these occur in modern individuals, thus indicating that such maladies have afflicted cetaceans for essentially their entire evolutionary history.

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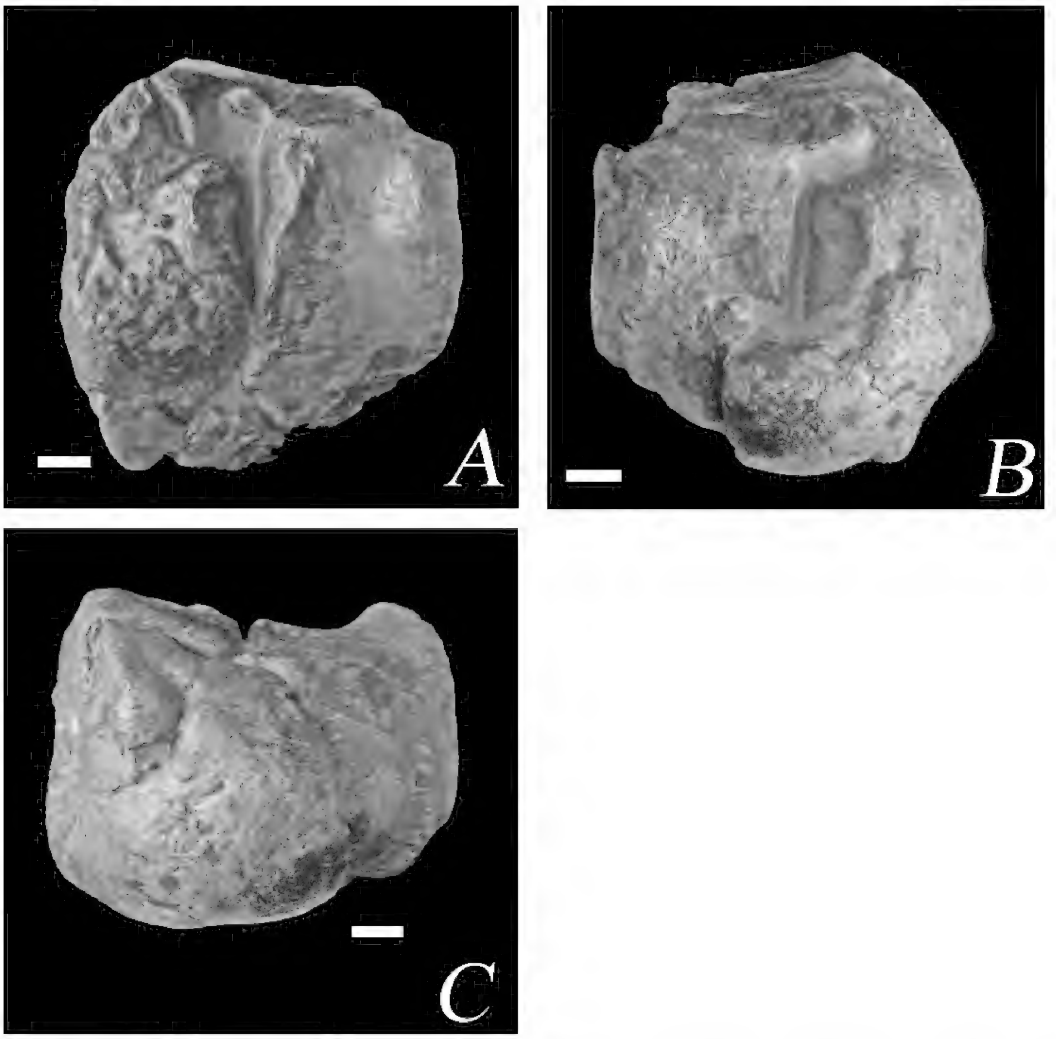

Figure 1 Mysticeti, gen. et sp. undet., two fused pathologic thoracic vertebrae, UWBM 87106, from the late Oligocene Pysht Formation, south side of the Strait of Juan de Fuca, Clallam County, Washington. **A**, left lateral view; **B**, right lateral view; **C**, ventral view. Scale bars = 2 cm.

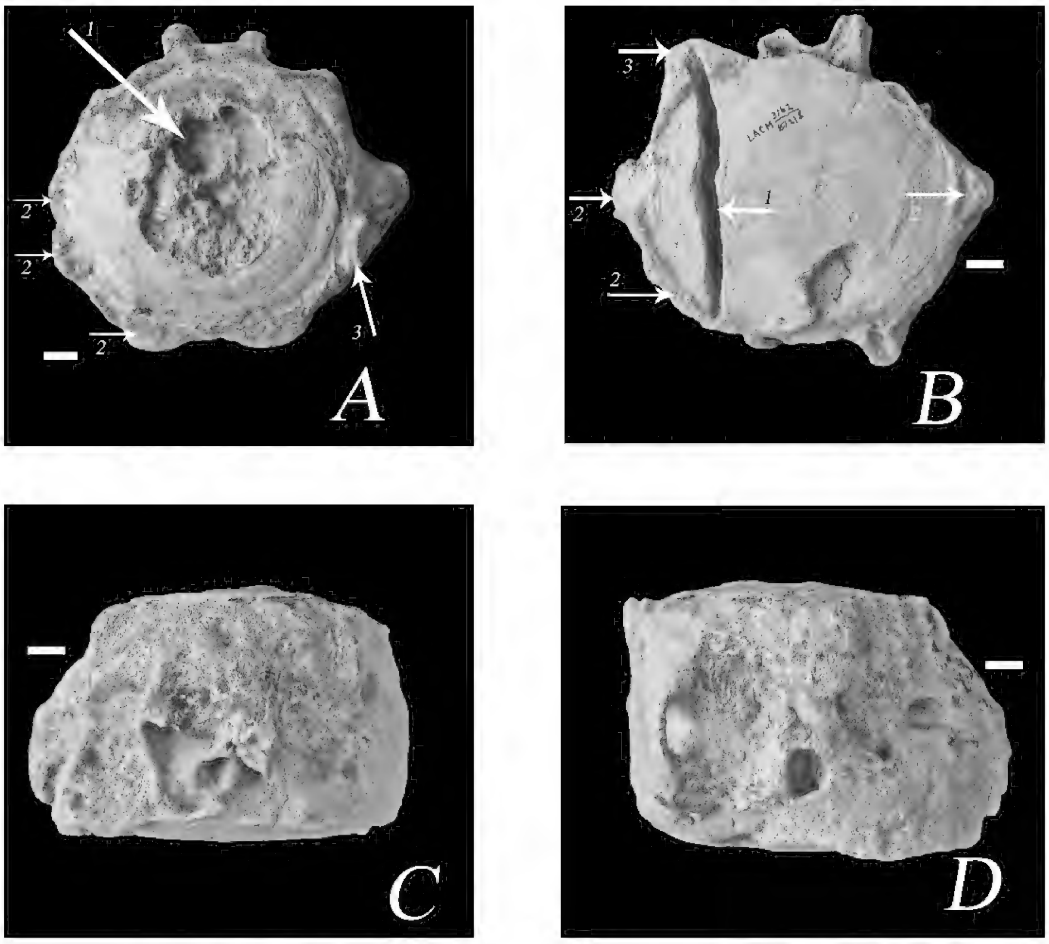

Figure 2 Mysticeti, gen. et sp. undet., pathologic caudal vertebra, LACM 151218, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A**, anterior view: 1 - indicates area possibly affected by a *Brucellosis*-type of bacterium, 2 - indicaes area of osteophytes, 3 - indicates osteophyte on the left side of the bone; **B**, posterior view: 1 - showing the break, 2 - showing osteophytes, 3 - showing the healing at the edge of the break; **C**, dorsal view: **D**, ventral view. Scale bars = 2 cm.

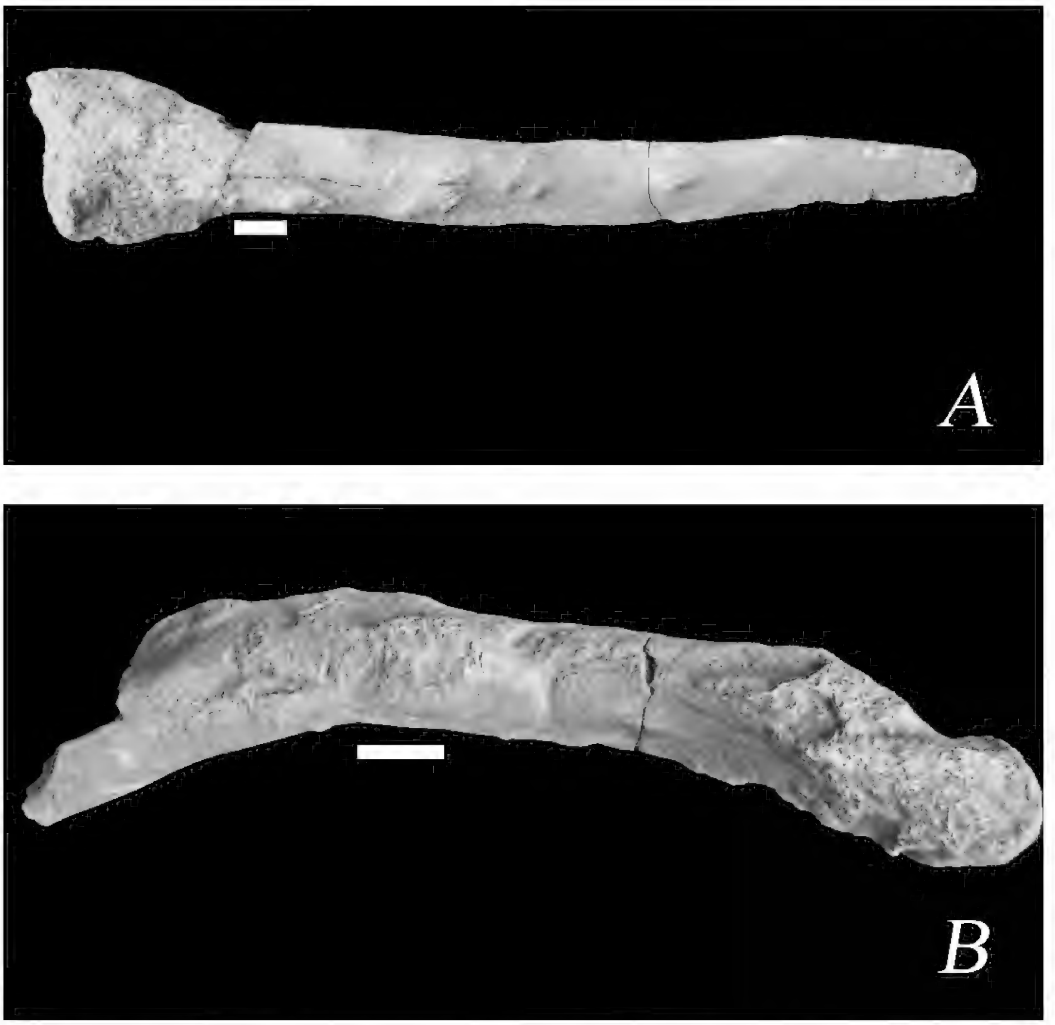

Figure 3 Mysticeti, gen. et sp. undet., pathologic ribs from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A**, LACM 48876 in medial view; **B**, LACM 150323 in anterior view. Scale bars = 2 cm.

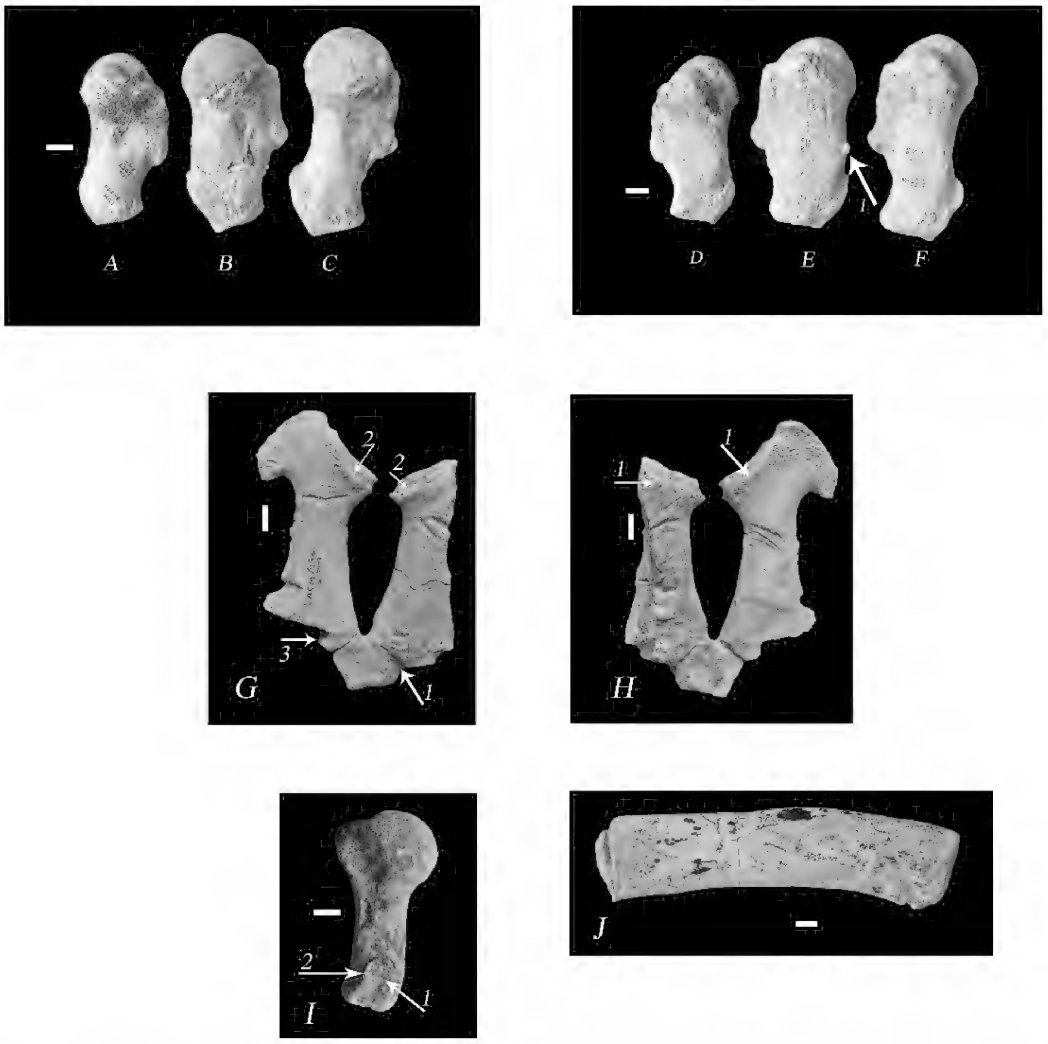

Figure 4 *Aulophyseter morricei* Kellogg, 1927b, referred specimens from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A and D**, right humerus, LACM 21184, in lateral and medial views; **B and E**, right humerus, LACM 127712, in lateral and medial views: **E**1 - arrow points to the osteoid osteoma; **C and F**, right humerus, LACM 21247: **C** - lateral and **F** - medial views, all showing osteophytes around the margins of the distal trochleae; **G and H**, pathologically fused radius, ulna, and proximal carpal bone, LACM 151243, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California: **G**, lateral view, 1 - showing area of fusion of radius to the proximal carpal, 2 - showing osteophytes, 3 - showing incomplete and dislocated distal epiphysis of the ulna; **H**, medial view, 1 - showing osteophytes, both views show shark tooth lacerations; **I**, Physeteridae, gen. et sp. undet., pathologic right humerus in posterior view, LACM 74077, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California: 1 - is the rough and pitted facet, 2 - is the bony bump on medial side of facet; **J**, Mysticeti, gen. et sp. undet., pathologic right radius, LACM 6443, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California, showing osteophytes and incompletely fused epiphysis. Scale bars = 2 cm.

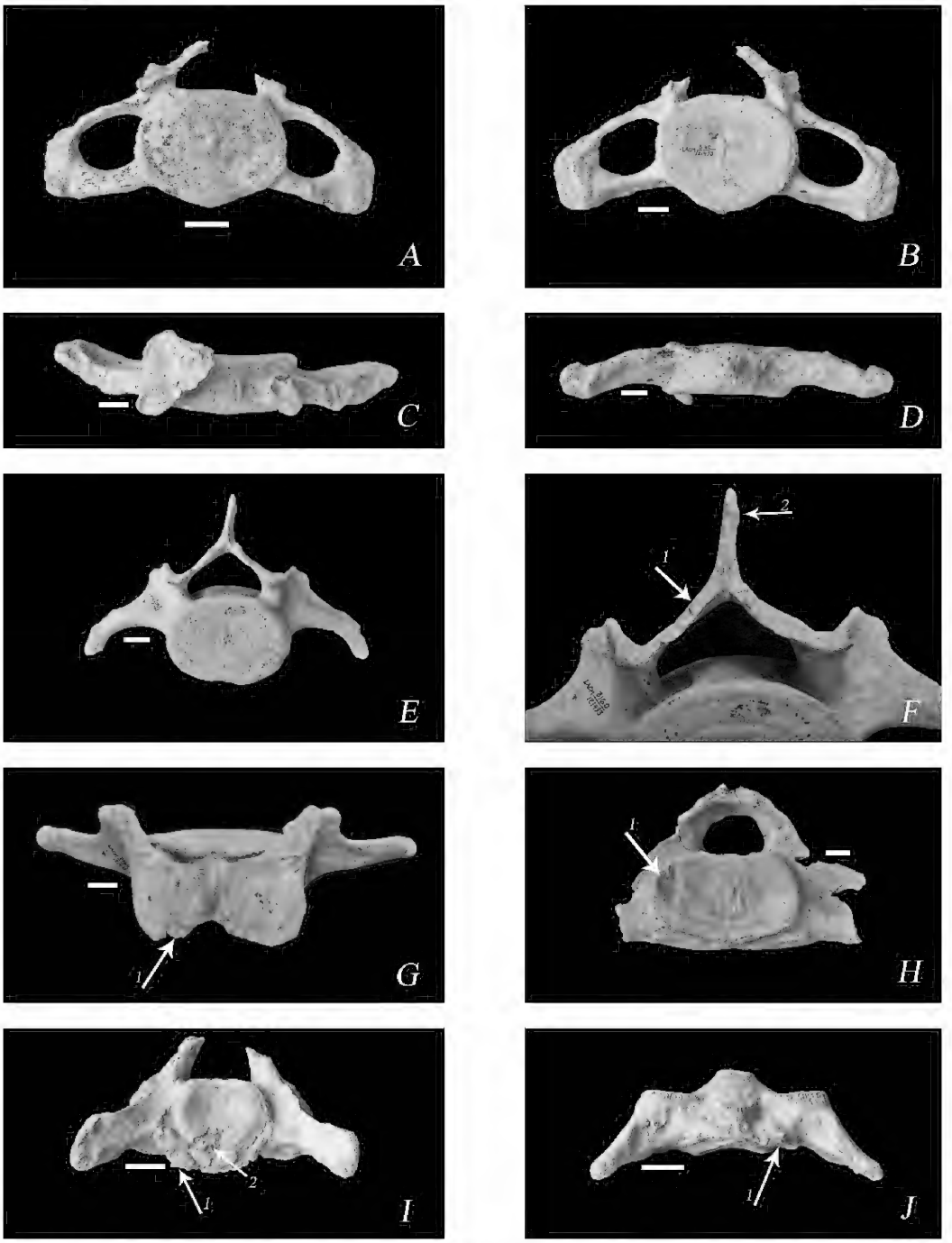

Figure 5 **A–H,** Mysticeti, gen. et sp. undet., pathologic cervical vertebrae, LACM 121493, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A–D**, probable third cervical vertebra: **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, ventral view; all views show bone deformations of the transverse process, the anterior and posterior views show the osteophytes; **E–G**, probable sixth cervical vertebra: **E**, posterior view; **F**, close-up of the dorsal process, 1 - indicates the area of hyperostotic bone growth, 2 - indicates the bone growth on the dorsal process; **G**, dorsal view, 1 - indicates the area of hyperostotic bone growth; **H**, pathologic axis vertebra, LACM 151230, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California; anterior view, 1 - arrow points to the depression in the right side of the centrum; **I and J**, ?Kentriodontidae, gen. et sp. undet., axis vertebra, LACM 151219, from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California: **I**, posterior view, 1 - showing extensive osteophytosis, 2 - showing broken epiphysis; **J**, ventral view, 1 - showing bony projection on the ventral surface of the right transverse process. Scale bars = 2 cm.

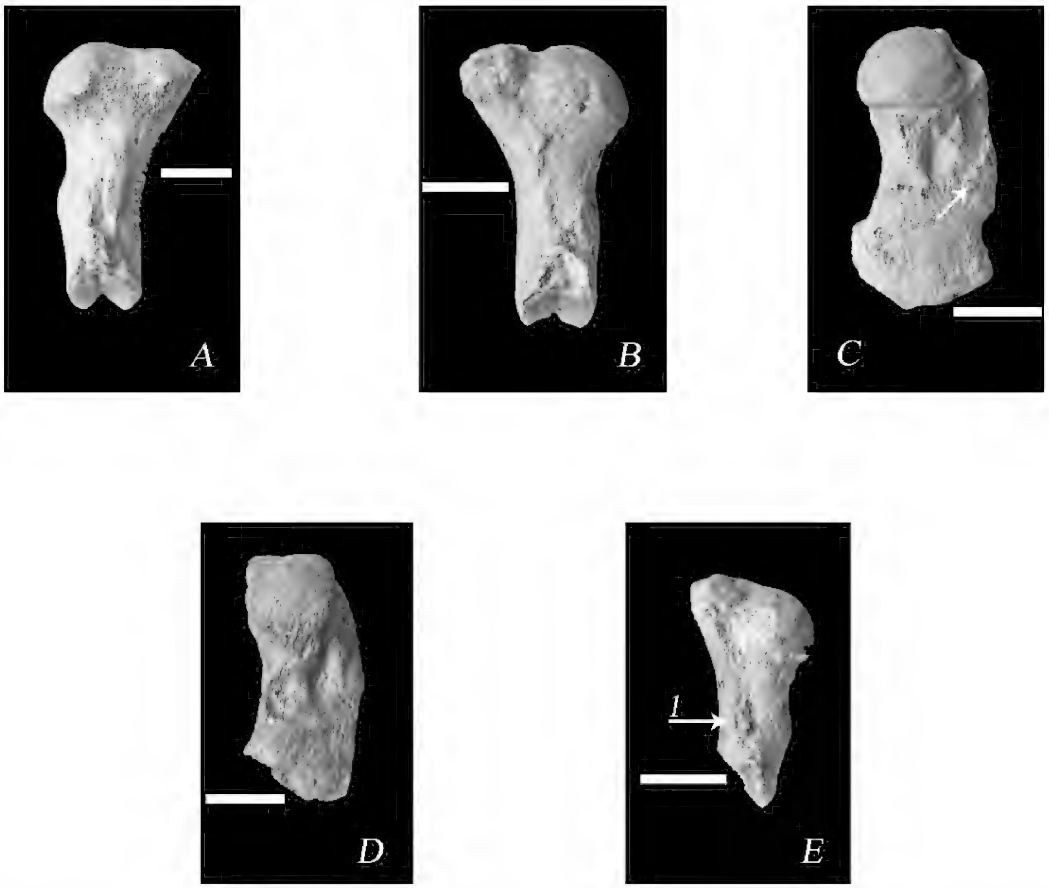

Figure 6 ?Kentriodontidae, gen. et sp. undet., pathologic humeri from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A**, left humerus, LACM 151220, in posterior view showing broken fusion at apex of olecranon process; **B and C**, right humerus, LACM 151240: **B**, posterior view showing rugose bone growth around greater tuberosity; **C**, lateral view showing small bony growth on the deltoid crest; **D**, right humerus, LACM 151246, lateral view showing ovoid depression on lateral surface of diaphysis; **E**, right humerus, LACM 151245, from the late Miocene Monterey Formation in Orange County, California, dorsal view, 1 - showing myositis scar. Scale bars = 2 cm.

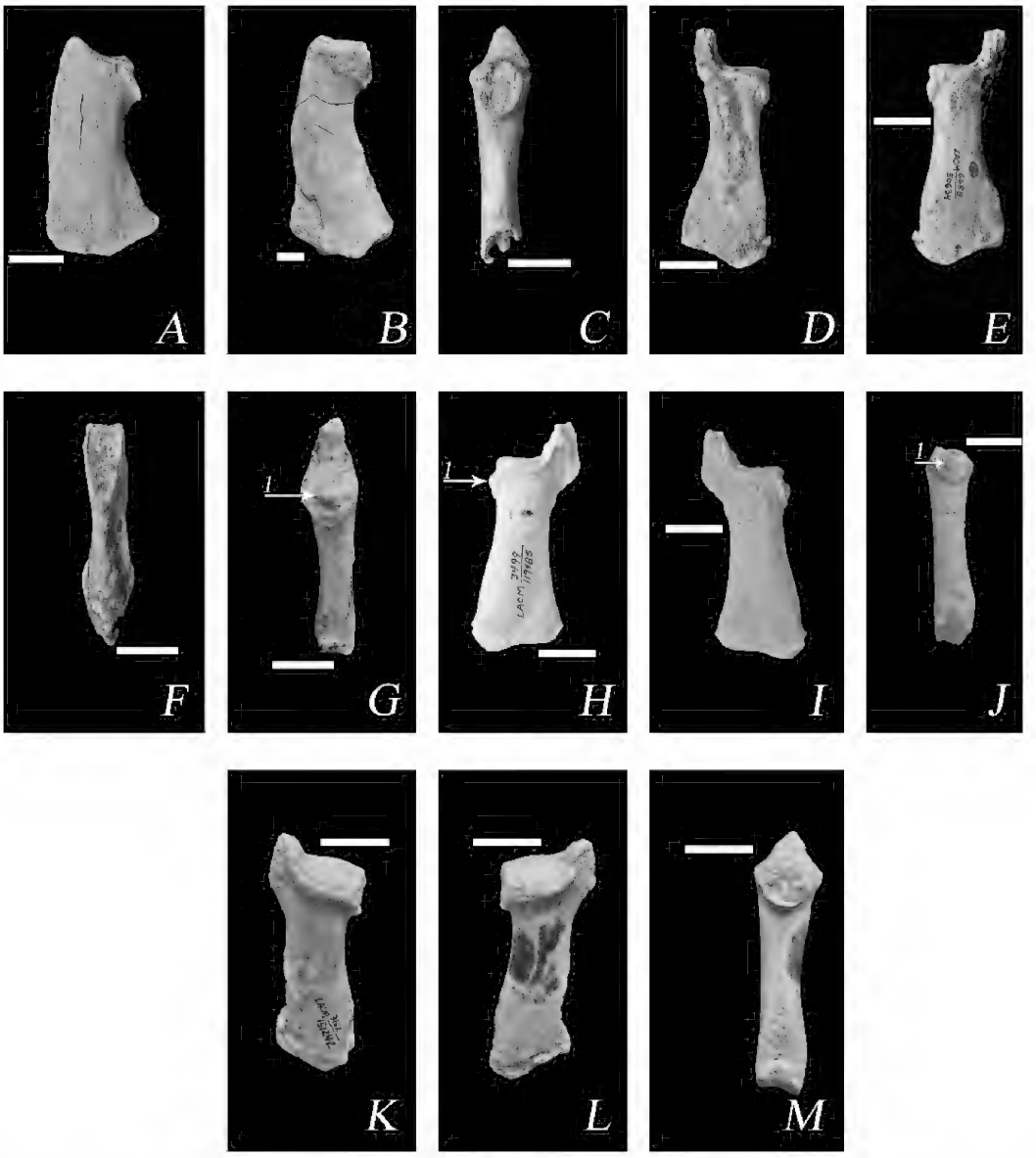

Figure 7 Pathologic odontocete limb bones from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A**, ?Kentriodontidae, gen. et sp. undet., right radius, LACM 45339, showing osteophytes and hyperostotic lipping; **B**, *Aulophyseter morricei* Kellogg, 1927b, referred left radius, LACM 74061, showing deep shark tooth lacerations; **C**, ?Kentriodontidae, gen. et sp. undet., left ulna, LACM 41468, with deformed radial facet; **D–G**, ?Kentriodontidae, gen. et sp. undet., right ulna, LACM 50634, with osteophyte and hyperostotic lipping around all of the articulations: **D**, lateral view; **E**, medial view; **F**, distal view; **G**, proximal view, 1 - showing the bony bump at the proximal margin of the radial facet; **H–J**, ?Kentriodontidae, gen. et sp. undet., right ulna, LACM 119485: **H**, medial view showing osteophytes around the humeral and radial articulations, 1 - the boney bump on the proximal radial facet; **I**, lateral view; **J**, anterior view showing, 1 - bone deformation on the proximal humeral facet; **K–M**, left ulna, LACM 151242: **K**, proximo-medial view showing osteophytes around proximal and distal articulating facets; **L**, proximo-lateral view showing osteophytes around proximal and distal articulating facets; **M**, anterior view showing pitted radial facet. Scale bars = 2 cm.

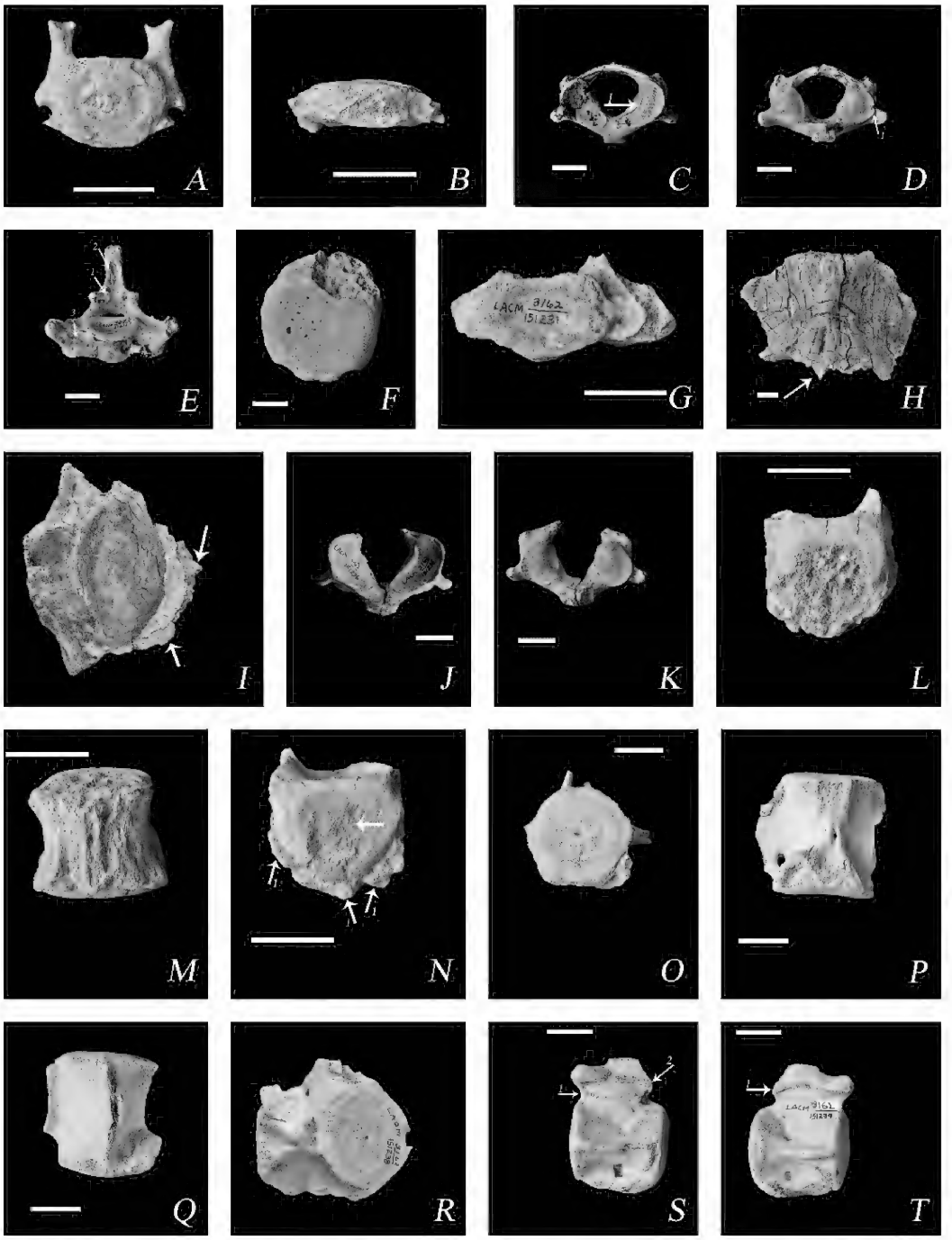

Figure 8 Cetacean pathologic vertebrae from the middle Miocene Sharktooth Hill Bonebed in the Round Mountain Silt in Kern County, California. **A–E**, Kentriodontidae, gen. et sp. undet., cervical vertebra, LACM 98789: **A**, anterior view; **B**, ventral view showing anteroposterior expansion of the vertebral body; associated atlas and axis vertebrae, LACM 115127; **C**, anterior view of atlas vertebra, 1 - showing fold in the left anterior facet; **D**, posterior view of atlas vertebra showing lipping around the posterior facet, 1 - the asymmetrical extension of right posterior facet; **E**, posteroventral view of axis vertebra indicating, 1 - excess bone growth on the left ventral side of the dorsal process, 2 - rugose bone growth on posterior side of dorsal process, 3 - bone spurs on ventral surface of vertebra; **F**, Mysticeti, gen. et sp. undet., caudal vertebra, LACM 151229, anterior view showing pitting on left dorsal margin; **G**, Kentriodontidae, gen. et sp. undet., cervical vertebra, LACM 151231, showing resorption on right posterior side; **H and I**, Mysticeti, gen. et sp. undet., lumbar vertebra, LACM 151232: **H**, ventral view; **I**, anterodorsal view; arrows

←

point to osteophytes; **J–T**, Kentriodontidae, gen. et sp. undet.: **J and K**, pathologic atlas vertebra, LACM 151236; **J**, anterior view, fold in left anterior facet; **K**, posterior view showing the lipping around both posterior facets; **L–N**, pathologic thoracic vertebra, LACM 151237: **L**, anterior view showing type of pitting attributable to *Brucellosis* infection; **M**, ventral view showing the striated exostotic growths; **N**, posterior view, 1 - indicates hyperostosis, 2 - indicates Schmorl's-like node; **O–R**, anterior caudal vertebra, LACM 151238, with hyperostotic bone growth on the right posteroventral portion of the centrum: **O**, posterior view; **P**, ventral view; **Q**, right lateral view; and **R**, anteroventral view; **S and T**, posterior caudal vertebra, LACM 151239: **S**, left lateral view, 1 - showing hyperostotic growth on the left pedicle, 2 - hyperostotic bone growth on the dorsal process; **T**, right lateral view, 1 - showing hyperostotic bone growth on dorsal process. Scale bars = 2 cm.

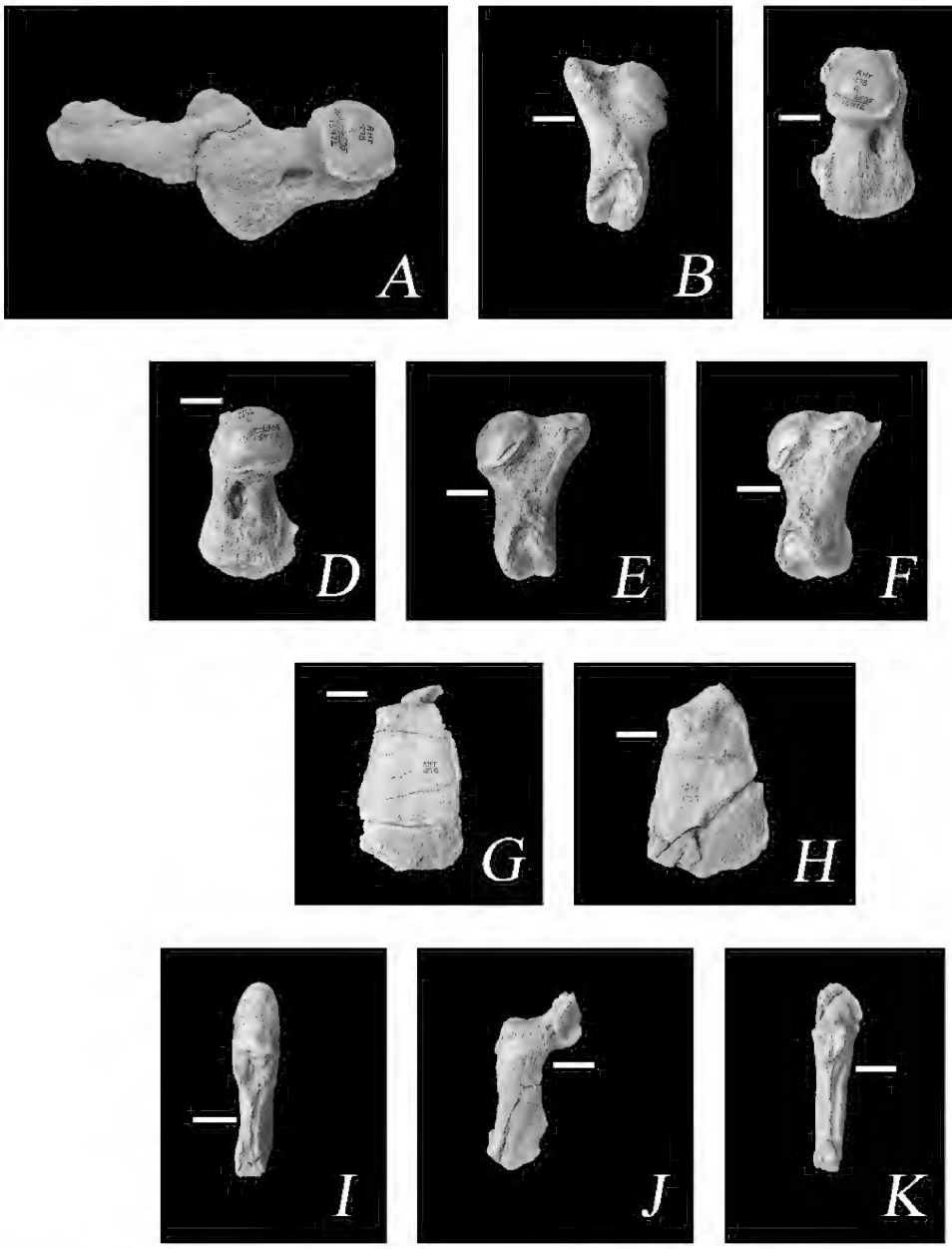

Figure 9 *Piscolithax tedfordi* Barnes, 1984, holotype, UCMP 315972 (formerly UCR 15972), from the latest Miocene Lower Member of the Almejas Formation on Isla Cedros, Baja California, Mexico. **A**, Right humerus and ulna articulated showing the pathologically fused elbow joint; **B**, posterior view of right humerus showing the break at the pathologically fused humerus–ulna articulation; **C**, lateral view showing osteoarthritic lipping around the humeral head; **D**, lateral view of left humerus; **E**, posterior view of left humerus showing the depression in the humeral head; **F**, posteromedial view of left humerus showing bone spur on greater tuberosity; **G**, medial view of left radius; **H**, lateral view of right radius; **I**, proximal view of right radius; **J**, medial view of right ulna showing osteophytes around the proximal articulation; **K**, anterior view of right ulna. Scale bars = 2 cm.

Early Clarendonian (late middle Miocene) fossil land mammal assemblages from the Lake Mathews Formation, Riverside County, Southern California, and a preliminary review of *Merychyus* (Mammalia, Artiodactyla, Oreodontidae)

E. Bruce Lander[1,2]

ABSTRACT. The first collection of fossil microvertebrate remains from the Miocene continental Lake Mathews Formation in Southern California represents five genera and five or six extinct species of small-bodied land mammals, including a leporid (*Hypolagus*), a sciurid (*Spermophilus* or *Ammospermophilus*), a heteromyid (possibly *Perognathus*), a geomyid (*Pliosaccomys*), and a cricetodontine murid (*Copemys esmeraldensis* and/or *Copemys russelli*). These taxa compose the Lake Mathews Sediment Basin No. 4 Local Fauna of the Cajalco Fauna. On the basis of the overlapping biochronologic ranges of *Ammospermophilus*, *Pliosaccomys*, and *Copemys*, this local fauna is late early Clarendonian to latest Clarendonian or early late Hemphillian in age, depending on which one of the two species of *Copemys* is present in the assemblage. The Borrow Area "C" Local Fauna of the Cajalco Fauna includes a medium-sized tapirlike ticholeptine oreodontid (*Merychyus medius compressidens*) and medium-sized and large camelids. On the basis of the shared occurrences of *M. medius compressidens*, the Borrow Area "C" Local Fauna is a correlative of the lower and middle parts the *Merychyus medius*/*C. russelli* Assemblage Zone in Member 2 of the Dove Spring Formation in the Mojave Desert of Southern California and the late early Clarendonian Minnechaduza Fauna from the lower part of the Ash Hollow Formation in north-central Nebraska and adjacent south-central South Dakota. Similarly, the Lake Mathews Sediment Basin No. 4 Local Fauna, if it contains *C. russelli*, might be another early late Clarendonian correlative of the *M. medius*/*C. russelli* Assemblage Zone, including the upper part of the zone occurring immediately above the tuff breccia unit that comprises the lower part of overlying Member 3 of the Dove Spring Formation. A third (unnamed) local fauna of the Cajalco Fauna is represented by a camelid and possibly a felid, and presumably is late early Clarendonian in age as well. The upper part of the Lake Mathews Formation is truncated by the Perris Surface. A probable outlier of this surface is overlain by the Basalt of Hogbacks, which has been determined to be as old as 11.91 ± 0.10 million years in age, on the basis of a ^{40}potassium–^{40}argon radiometric dating analysis. This and a number of other radiometric age determinations suggest that the Cajalco and Minnechaduza faunas are late middle Miocene in age, between 12.18 and 11.93 million years old, and possibly younger than the lower part of the *M. medius*/*C. russelli* Assemblage Zone in the lower part of Member 2 of the Dove Spring Formation.

INTRODUCTION

This report updates an earlier report by Lander and Whistler (2002) that summarized the results of the Metropolitan Water District of Southern California (Metropolitan) Cajalco Creek Dam and Detention Basin (CCDDB) Project paleontologic resource impact mitigation program. The mitigation program was conducted by Paleo Environmental Associates, Inc. (PEAI), personnel on behalf of Metropolitan during, and in support of, excavation and other earth-moving activities associated with construction of the CCDDB Project at Lake Mathews in Riverside County, Southern California. The mitigation program was required of Metropolitan, the California Environmental Quality Act (CEQA) lead agency for

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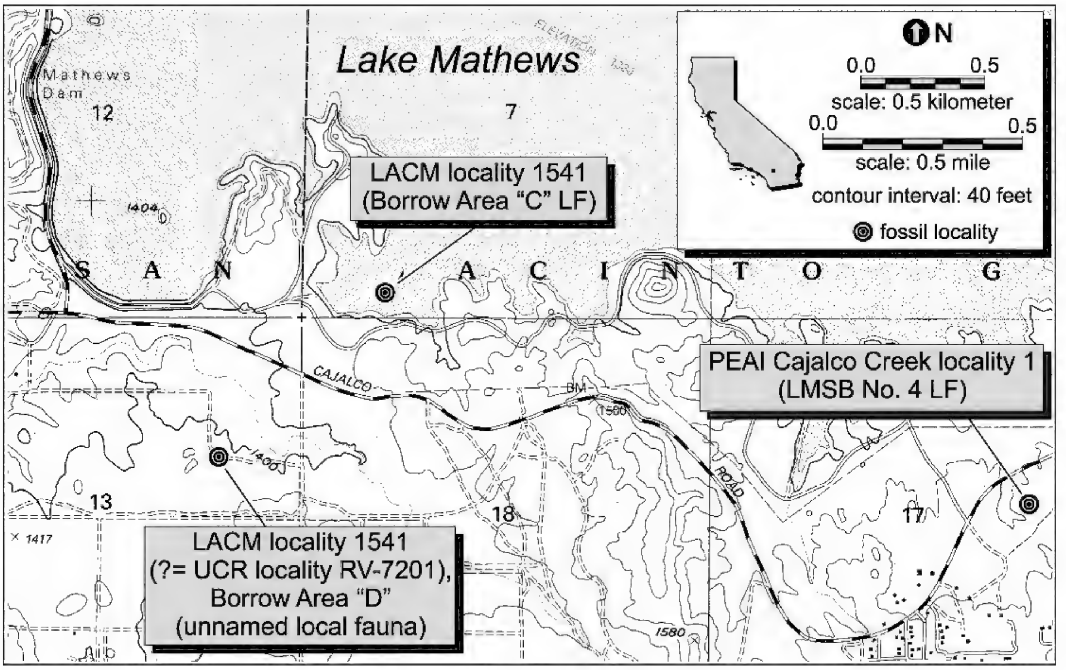

Figure 1 Locations of fossil localities and of fossil land mammal assemblages composing Cajalco Fauna, Lake Mathews Formation, Riverside County, California. Base map: U.S. Geological Survey Lake Mathews Quadrangle, California—Riverside County, 7.5-Minute Series (topographic) (1997).

the CCDDB Project, because of the potential for the loss of scientifically highly important fossil land mammal remains in the continental Lake Mathews Formation (LMF) as a result of these earth-moving activities. The program subsequently was implemented by PEAI personnel at the start of excavation to ensure project compliance with CEQA and Metropolitan Water District of Southern California Environmental Planning Branch (1998) standard paleontologic mitigation measures. These measures included paleontologic monitoring of earth-moving activities by a paleontologic construction monitor to allow for the recovery of any fossil remains that might have been exposed by these activities in areas underlain by the LMF.

Identifiable bones and teeth of eight genera and eight or nine extinct species of middle to late Miocene land mammals have been recovered at three or four previously recorded fossil localities in the LMF. Six of the genera are extinct. The fossil land mammal assemblage from each locality represents a local fauna, and the local faunas from these localities, in turn, comprise the Cajalco Fauna (Lander, 2004). Currently, these assemblages are recognized as separate local faunas because it has not been demonstrated conclusively that they occur at approximately the same stratigraphic level in the LMF, or even that they are assignable to the same North American Land Mammal Age (NALMA).

The first reported fossil collection of microvertebrate remains from the LMF was recovered as a result of processing a 2,727-kg sedimentary rock sample of the formation (Lander and Whistler, 2002; Lander, 2004). The sample, in turn, was collected from a 0.6-m-thick stratigraphic interval exposed by excavation of Lake Mathews Sediment Basin (LMSB) No. 4 (Lander and Whistler, 2002; Lander, 2004). Lake Mathews Sediment Basin No. 4, which was part of the CCDDB Project, lies along the southern side of Cajalco Road, immediately south of Lake Mathews (Fig. 1; Lander and Whistler, 2002; Lander, 2004). The LMSB No. 4 fossil locality lies approximately 2.6 km east-southeast and 3.1 km east of two previously recorded Natural History Museum of Los Angeles County, Department of Vertebrate Paleontology (LACM) fossil localities in the borrow areas (Borrow Areas "C" and "D," respectively) that provided the fill used in the enlargement of Mathews Dam at the western end of Lake Mathews (Fig. 1; Proctor, 1961, 1962; Proctor and Downs, 1963; Lander and Whistler, 2002). Both localities have been cataloged as LACM locality 1541. Large-bodied land mammal species are represented by fossilized bones and teeth that were recovered from freshly exposed bedrock in the two borrow areas, from the transported fill that was excavated from these borrow areas, and possibly from a third nearby

borrow area. However, only the Borrow Area "C" Local Fauna (LF) and the LMSB No. 4 LF contain comparatively age-diagnostic land mammal taxa that can be assigned relatively confidently to just one or two North American land mammal ages.

METHODS AND MATERIAL

ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York USA
Ar/Ar	^{40}argon/^{39}argon single-crystal laser fusion
AZ	assemblage zone
CCDDB	Cajalco Creek Dam and Detention Basin
CEQA	California Environmental Quality Act
CGS	California Geological Survey (formerly California Division of Mines and Geology)
CMNH	Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania USA
CPT	Cougar Point Tuff Unit
DSF	Dove Spring Formation
DVP	former Vertebrate Paleontology Department, AMNH
F:AM	Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York USA
FTM	Fossiliferous Tuff Member
K-Ar	^{40}potassium–^{40}argon
LACM	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA
LF	Local Fauna
LMF	Lake Mathews Formation
LMSB	Lake Mathews Sediment Basin
Metropolitan	Metropolitan Water District of Southern California
MFA	Myra L. Frank & Associates, Inc. (now Jones & Stokes)
NALMA	North American Land Mammal Age
O.R.	observed range
PEAI	Paleo Environmental Associates, Inc., Altadena, California USA
PUM	Princeton University Museum of Natural History (collection now at Peabody Museum, Yale University), New Haven, Connecticut USA
RBM	Resistant USA Breccia Member
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
UCR	Department of Geological Sciences, University of California, Riverside, California USA (collections and records now maintained at UCMP)
UNSM	University of Nebraska State Museum, Lincoln, Nebraska USA
USGS	United States Geological Survey
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. USA
WCAP	Western Center for Archaeology and Paleontology, Hermet, California USA

Under a storage agreement between the Metropolitan Water District of Southern California (Metropolitan) and the Western Center for Archaeology and Paleontology (WCAP) at Diamond Valley Lake in Hemet, Riverside County, California, the fossil remains from Lake Mathews Sediment Basin (LMSB) No. 4 are part of the WCAP fossil collection. Accordingly, the fossil remains will be cataloged as WCAP specimens. However, under the agreement, Metropolitan retains ownership of the specimens.

The systematics of the ticholeptine oreodontid *Merychyus* Leidy, 1859, discussed in this report follow Lander (1998, 2004, 2005a, 2005b). The length of the P1–M3, in combination with morphologic features of the skull (particularly degree of retraction of external narial opening), is used in this report to combine or differentiate stratigraphically restricted samples assigned to *Merychyus medius* Leidy, 1859, and *Merychyus major* Leidy, 1859. P1–M3 length is regarded as a reliable indicator of adult body size in oreodontids because this measurement is correlated strongly with skull length, which, in turn, is correlated with adult body size (Lander, 1977; Stevens and Stevens, 1996). However, differences in P1–M3 length between successive samples are not used to recognize different species. Average adult body size in oreodontids, including *Merychyus*, often fluctuated dramatically through time (Lander, 1977, 1984, 1985, 1988, 1989, 1998; Prothero, 1982, 1985; Kelly and Lander, 1988; Lander and Kelly, 1989; Prothero and Heaton, 1996; Stevens and Stevens, 1996; Prothero and Schoch, 2002), whereas contemporary changes in their cranial and dental morphologies, if any, usually were very limited (Lander, 1977). Lander (1977, 1984, 1988, 1989, 1998) considered such fluctuations in oreodontid body size to be phenotypic responses to climatically induced fluctuations of their food supply. Therefore, following Lander (1998), morphologically similar samples of *Merychyus* that differ substantially in their mean P1–M3 lengths are assigned to the same species, but to different subspecies. The recognition of two or more morphologically

North American Land Mammal Age	Ma	Stratigraphic Unit/Land Mammal Assemblage: Ogallala Formation/Group, Texas & Oklahoma	Ogallala Formation/Group, South Dakota, Nebraska, Kansas, & Colorado	Dove Spring & Barstow Formations, California	*Merychyus* Biochron
Early Late (type) Hemphillian	6.90[a]	Coffee Ranch Local Fauna (TX) (type)	**ZX Bar Local Fauna (NE)**		*M. major*?, new subspecies (large)
Late Early (type) Hemphillian		? ? ?	***Aphelops* Draw Fauna (NE)**		
	7.80[b]	Higgins LF (TX) (type)	? ? ?		? ? ?
	8.32[c] 8.50[d]	Arnett LF (OK)		*Paronychomys/ B. littoralis* AZ 5 middle	
Earliest Hemphillian	8.70[e]	Capps Pit LF (OK)?	**Snake Creek Fauna (NE)**	lower	*M. ma.*? *profectus*
Latest Clarendonian / Type Montediablan	9.36[f]	**"Upper" Coetas Creek Fauna (TX)**	***Alligator mefferdi* Quarry LF & Murphy Member fauna? (NE)**	***Epicyon haydeni/ Hipparion forcei* AZ**	*M. major major*
	11.10[g] 11.19,			***Cupidinimus avawatzensis/ Paracosoryx furlongi* AZ** 4 upper	
Early Late (type) Clarendonian	11.55[h]	Gidley's 3-toed Horse Quarry LF (TX) (type)	**Xmas-Kat Quarries (NE) & Lenora Local Faunas (KS)** 7	middle ? ?	*M. major*, new subspecies (large)
Middle Clarendonian	11.93[i]		**Big Spring Canyon (SD) & George Creek LFs (CO)**	lower	*M. medius santacruzensis*
Late Early Clarendonian / ? ? ? Type Cerrotejonian		**Couch Ranch Local Fauna (TX)**	**Minnechaduza (NE, SD) & Mission Faunas (SD)**	***M. medius/C. russelli* AZ** middle ? ?	*M. medius compressidens*
Middle Early Clarendonian / ? ? ? (= latest Valentinian)	12.18[j]	**Bivins Ranch Local Fauna (TX)**	**Burge Fauna (NE)** 6	3 ? ? ? lower	*M. medius novomexicanus*
Earliest (type) Clarendonian		**Lower Clarendon Fauna (TX) (type)**	**Devil's Gulch Fauna (NE)**		*M. medius medius* (large)
Latest Barstovian	12.60[k]		**Niobrara River Fauna (NE, SD) & Vim-Peetz Local Fauna (CO)**	? ? ? Cronese Local Fauna	*M. medius medius* (medium sized)
Early Late Barstovian (= earliest Valentinian)	13.55[l]		**Norden Fauna (NE) & Kennesaw Local Fauna (CO)**	Upper Barstow Fauna	*M. medius medius* (small)
Early (type) Barstovian	14.00[m] 14.81[n]		**Fort Randall Fm. fauna (NE), N/S Bijou Hill LFs (SD), Densmore S LF (KS), & Keota Fauna (CO)**	Lower Barstow Fauna (type) 2	*M. medius? schrammi*
Latest Hemingfordian	15.28[o] 15.55,			Second Division Fauna	? ? ?
	15.88[p]		**Lower Snake Creek Fauna (NE)**	**Upper Green Hills Fauna**	
Early Late (type) Hemingfordian	16.30[q]		**Sheep Creek (NE) (type) & Eubanks Faunas (CO)**	Lower Green Hills Fauna 1	*M. relictus* ? ? ?

Figure 2 Correlation of some late Hemingfordian to early late Hemphillian oreodontid-bearing fossil land mammal assemblages from the western half of United States. Assemblages with names in bold type contain *Merychyus*. In part after Lander (1985, 2005b), Evander (1986), and Tedford et al. (1987, 2004).

Sources of radiometric age determinations: **a**, Ar/Ar (converted), Coffee Ranch Ash, just above Coffee Ranch Quarry LF, Ogallala Formation, Hemphill County, Texas (Izett and Obradovich, 2001; Tedford et al., 2004); **b**, K-Ar, Warm Springs Tuff Member, above earliest Hemphillian Lower Alturas Fauna, Alturas Formation, Modoc County, California (Luedke and Smith, 1981); **c**, K-Ar (converted), Rattlesnake Butte Tuff, below Lower Alturas Fauna, base of Alturas Formation (Evernden et al., 1964, sample KA 1262); **d**, K-Ar, tuff unit Tra-16, between lower and middle parts of *Paronychomys/Borophagus littoralis* AZ, and Member 6, DSF, Kern County, California (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, section E, fig. 4); **e**, K-Ar, Happy Valley Tuff, 350 m above base of Orinda Formation, Contra Costa County, California (G.H. Curtis, personal communication, 1977, in Creely et al., 1982, sample KA-3013); **f**, interpolation, tuff unit Tra-15, near top of *Epicyon haydeni/Hipparion forcei* AZ, base of Member 6, DSF (Whistler and Burbank, 1992:fig. 3, sections B, C, E, fig. 4; Perkins et al., 1998:fig. 3, sample epb92-75); **g**, interpolation (10.5 ± 0.25 Ma in age on basis of K-Ar radiometric dating analysis), upper basalt unit, between *Cupidinimus avawatzensis/Paracosoryx furlongi* and *E. haydeni/H. forcei* AZs, Member 4, DSF (Whistler and Burbank, 1992:fig. 3, section D, fig. 4; Perkins et al., 1998:fig. 3, sample "basalt"); **h**, interpolation, tuff unit Tra-6, near bases of upper part of *C. avawatzensis/P. furlongi* AZ and middle part of Member 4 (between lower and upper basalt units), DSF (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, sections D and E, fig. 4; Perkins et al., 1998:fig. 3, sample epb92-30); K-Ar, Davis (?= *Machaerodus*) Ash, above Minnechaduza Fauna and possibly Xmas–Kat LF, middle part, Merritt Dam Member, Ash Hollow Formation, Ogallala Group, Cherry County, Nebraska (Skinner and Johnson, 1984; Swisher, 1992; Alroy, 2002; Tedford et al., 2004); **i**, Ar/Ar, Ibex Hollow Ash (?= tuff unit Tra-2), lower part of *C. avawatzensis/P. furlongi* AZ, middle part of Member 3, DSF (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, sections A, D–F; Perkins et al., 1998, samples epb94-580 and tc89-21a); **j**, K-Ar, Swallow Ash, near base of Minnechaduza Fauna and 1 m above base of Cap Rock Member, Ash Hollow Formation (Skinner and Johnson, 1984; Swisher, 1992; Tedford et al., 2004); **k**, Ar/Ar, Cronese Tuff, below Cronese LF, Barstow Formation, San Bernardino County, California (Swisher, 1992; Tedford et al., 2004); **l**, Ar/Ar, Hurlbut Ash, bracketed by Norden Fauna, 7.9 m above base of Cornell Dam Member, Valentine Formation, Ogallala Group, Brown County, Nebraska (Skinner and Johnson 1984; Swisher 1992; Tedford et al., 2004); **m**, Ar/Ar, *Hemicyon* Tuff, between Lower and Upper Barstow faunas and lower and upper parts of FTM, Barstow Formation (MacFadden et al., 1990; Woodburne et al., 1990; Woodburne, 1991, 1996; Tedford et al., 2004); **n**, Ar/Ar, Dated Tuff, 17 m above base of Barstow Fauna and top of Skyline Tuff at base of FTM (MacFadden et al., 1990; Woodburne et al., 1990; Woodburne, 1991, 1996; Tedford et al., 2004); **o**, Ar/Ar, Valley View Tuff, between Green Hills and Second Division faunas, RBM, Barstow Formation (C.C. Swisher III, personal communication, 1991, in Woodburne, 1991, 1996); **p**, interpolation, Sheep

similar subspecies under the same species provides a means of identifying and uniting samples of comparable body size, while distinguishing them from a morphologically similar sample of larger or smaller body size and a slightly different geologic age.

Numerous *Merychyus* specimens in the Frick Collection at the Department of Vertebrate Paleontology, American Museum of Natural History (F:AM), most from the Valentine and Ash Hollow formations of the Ogallala Group in north-central Nebraska and adjacent south-central South Dakota were measured for this study, which also relied heavily on measurements presented by Schultz and Falkenbach (1941:tables 1 and 9). Stratigraphic data for these specimens were presented by Skinner et al. (1968) and Skinner and Johnson (1984) or were provided to the author by the late Morris F. Skinner (written communication, 1973), then Frick Curator Emeritus in the Vertebrate Paleontology Department (DVP) of the AMNH. Most of these specimens were published by Schultz and Falkenbach (1941), whereas most of the remainder of the F:AM specimens that were not reported by Skinner and Johnson (1984) were cataloged at the AMNH specifically for this study. Often, the stratigraphic data published by Schultz and Falkenbach (1941) were inaccurate or incorrect (Skinner et al., 1968; M.F. Skinner, written communication, 1973; Skinner and Johnson, 1984).

The subdivisions of the Dove Spring Formation (DSF) used in this report are after Whistler and Burbank (1992). The North American Land Mammal Ages of Wood et al. (1941), as recognized in this report, follow Evander (1986) (but not Tedford et al., 1987, 2004), with respect to the Hemingfordian–Barstovian NALMA boundary in the Hemingfordian and Barstovian NALMA stratotypes, and Lander (1985, 2004, 2005a, 2005b), with regard to the Barstovian–Clarendonian and Clarendonian–Hemphillian NALMA boundaries, the subdivisions of the Clarendonian and early Hemphillian NALMAs, and correlation of their respective fossil land mammal assemblages.

The Barstovian NALMA is based specifically on the assemblages (Barstow Fauna) from stratigraphically above the Skyline Tuff in the Fossiliferous Tuff Member (FTM) of the Barstow Formation in San Bernardino County, Southern California (Wood et al., 1941). Correspondingly, Lander (1977, 1985, 2005b), Evander (1986), and Kelly and Lander (1988), contrary to Tedford et al. (1987, 2004) and most other workers, assigned the assemblages (particularly Lower Green Hills Fauna) from below the Skyline Tuff in the underlying Resistant Breccia Member (RBM) to the Hemingfordian NALMA rather than to the Barstovian (Fig. 2).

As recognized by Lander (2005b) and in this report (Fig. 2), the type Barstovian fauna, again contrary to Tedford et al. (1987, 2004) and most other workers, is restricted to the Lower Barstow Fauna, which occurs in the lower part of the FTM and is bracketed stratigraphically by the Skyline Tuff below and the *Hemicyon* Tuff above (Lander, 2005b). The *Hemicyon* Tuff lies approximately 75 to 82 m above the Skyline Tuff (Woodburne et al., 1990). According to Tedford et al. (2004), correlatives of the Lower Barstow Fauna include the Keota Fauna from the upper part of the Pawnee Creek Formation in the Ogallala Group of northeastern Colorado (Fig. 2). At the time the Barstovian NALMA was defined by Wood et al. (1941), none of the taxa that were designated as Barstovian index taxa, or were stated to have had their first occurrences during the Barstovian, had been reported previously from above the *Hemicyon* Stratum in the upper part of the FTM. On the other hand, the ursid *Hemicyon* Lartet, 1851, on the basis of the record of *Hemicyon barstowensis* Frick, 1926, then was known locally only from the *Hemicyon* Stratum (Frick, 1926), which, according to Woodburne et al. (1990), lies about 3 to 30 m below the *Hemicyon* Tuff. *Hemicyon* is one of the taxa Wood et al. (1941) designated as a Barstovian index taxon. According to Hunt (1998), *H. barstowensis* is assignable to *Plithocyon* Ginsburg, 1955. Presumably, this species includes *Hemicyon californicus* Frick, 1926, also from the *Hemicyon* Stratum (Frick, 1926).

Assemblages of late (post type) Barstovian age, as recognized by Lander (2005b) and in this report, include the Upper Barstow Fauna, which occurs above the *Hemicyon* Tuff. According to Tedford et al. (2004), early Valentinian faunas from the Cornell Dam and Crookston Bridge

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interpolation, Sheep Creek Ash No. 3, between upper Sheep Creek and Lower Snake Creek faunas, upper member, Sheep Creek Formation, Hemingford Group, Sioux County, Nebraska (Skinner et al., 1977:fig. 4C; Perkins and Nash, 2002:tables 3, DR2); K-Ar, Oreodont Tuff, between Lower and Upper Green Hills faunas, RBM (MacFadden et al., 1990; Woodburne et al., 1990; Woodburne, 1991, 1996; Tedford et al., 2004); **q**, K-Ar, Rak Tuff, below Green Hills Fauna, top of Owl Conglomerate Member, Barstow Formation (MacFadden et al., 1990; Woodburne et al., 1990; Woodburne, 1991, 1996; Tedford et al., 2004).

Stratigraphic boundaries of faunal assemblages: **1**, Oreodont Tuff; **2**, *Hemicyon* Tuff; **3**, tuff unit Tra-1, near middle of Member 2, DSF (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, sections E and F, fig. 4); **4**, tuff unit Tra-6; **5**, tuff unit Tra-16; **6**, Swallow Ash; **7**, Davis (?= *Machaerodus*) Ash.

members in the lower part of the Valentine Formation in north-central Nebraska and south-central South Dakota are correlatives of the Upper Barstow Fauna (Fig. 2; see Schultz and Stout [1961] and Schultz et al. [1970] regarding definition of Valentinian Provincial [Land Mammal] Age). Age-diagnostic land mammal taxa, such as the cricetodontine murids *Copemys russelli* (James, 1963) and *Copemys esmeraldensis* Clark, Dawson, and Wood, 1964, first appear locally above the *Hemicyon* Tuff (Lindsay, 1972). Lander (2004) mistakenly considered the first appearances of *C. russelli* and *Pliosaccomys* Wilson, 1936, to be early Barstovian in age.

The UCMP on-line collections database was used for documenting the occurrences of age-diagnostic land mammal taxa at particular UCMP fossil localities, whereas the paleobiology database of the National Center for Ecological Analysis and Synthesis (J. Alroy, database coordinator) was used to conduct the task for these localities and for those localities that yielded land mammal remains contained in the collections of other institutions.

GEOLOGY OF THE LAKE MATHEWS AREA

Surficial geologic mapping of the area surrounding Lake Mathews (including the Cajalco Creek Dam and Detention Basin [CCDDB] Project site and Borrow Areas "C" and "D") is presented at scales of 1:24,000 by Morton (2001) and Morton and Weber (2001), 1:100,000 by Morton (2004), 1:240,000 by Woodford et al. (1971), and 1:250,000 by Rogers (1965). Lake Mathews lies near the northwestern corner of the Perris Block in the northern Peninsular Ranges Province, where major linear geologic structures (faults, folds) and the resulting geographic features (mountains, valleys) trend in a predominantly northwesterly direction (Jahns, 1954; Proctor, 1961, 1962; Rogers, 1965; Morton and Gray, 1971; Woodford et al., 1971; Morton and Weber, 2001; Morton, 2004). The Perris Block is a narrow fault-bounded crustal block that is bounded to the northeast by the San Jacinto Fault Zone, to the southwest by the Elsinore Fault Zone, and at its northwestern end by a series of faults, including the Cucamonga Fault, that form the southern boundary of the Transverse Ranges Province, in which major geologic structures and geographic features trend in a predominantly east–west direction (Jahns, 1954; Proctor, 1961; Rogers, 1965; Morton and Gray, 1971; Woodford et al., 1971; Morton and Matti, 1989; Morton, 2004).

Surficial geologic mapping by Proctor (1961), Morton (2001, 2004), and Morton and Weber (2001) indicate that much of the area surrounding Lake Mathews (including LMSB No. 4 site prior to excavation) is underlain by a thin discontinuous sheet of early to middle Pleistocene alluvial fan deposits (terrace deposits of Proctor, 1961). These deposits, usually only several centimeters to a meter in thickness, might be as much as 6 to 12 m in thickness locally (Proctor, 1961; Woodford et al., 1971). The surficial mapping, along with subsurface geologic mapping of the area (including LMSB No. 4 site) by Proctor (1961), indicates that the alluvial fan deposits are underlain by lacustrine and fluvial strata composing the Lake Mathews Formation (LMF), and that this formation, in turn, is separated by a major erosional unconformity from the underlying monzogranite of the early late Cretaceous Cajalco Pluton (part of Southern California Batholith) (Proctor and Downs, 1963; Woodford et al., 1971; Lander and Whistler, 2002; Morton, 2004). The LMF fills previously existing topographic depressions on, and a channel cut into, the irregular erosional surface at the top of the pluton (Proctor, 1961, 1966; Proctor and Downs, 1963; Woodford et al., 1971). The undulating erosional surface that separates the Cajalco Pluton and the LMF from the overlying alluvial fan deposits is the Perris Surface (Woodford et al., 1971). Approximately 25 km southeast of Lake Mathews, a probable outlier of the Perris Surface is overlain by the Basalt of Hogbacks, which has been determined to be as old as 11.91 ± 0.10 Ma in age on the basis of a whole-rock ^{40}potassium–^{40}argon (K-Ar) radiometric dating analysis (Kennedy [1977] sample KA–5; converted by Morton and Morton [1979] using revised decay and abundance constants provided by Dalrymple [1979]). These radiometric age determinations suggest that the LMF is older than 11.91 Ma in age.

The LMF was described and named by Proctor (1961) in an unpublished Metropolitan report and subsequently was defined formally by Woodford et al. (1971). The formation, at least 89 m in thickness and approximately 15.5 km^2 in areal extent, consists mostly of massive white to greenish-gray and light green claystone, mudstone, siltstone, and silty fine-grained sandstone layers that are interbedded with poorly to well-bedded and cross-bedded, white to gray, medium- to coarse-grained sandstone, pebbly sandstone, and conglomerate layers (Proctor, 1961, 1962, 1966; Proctor and Downs, 1963; Woodford et al., 1971; Morton, 2001, 2004; Morton and Weber, 2001). As indicated by surficial geologic mapping by Morton and Weber (2001) and Morton (2004) and subsequently confirmed by Paleo Environmental Associates, Inc. (PEAI), paleontologic construction monitors, the LMF was not exposed at the LMSB No. 4 site prior to the excavation of the basin as a part of CCDDB Project construction. Excavation of the basin exposed the formation, the local top of which was observed to lie unconformably below a 0.15-m-thick cover of alluvial fan deposits.

Pronounced inconsistencies were documented by Lander and Whistler (2002) among the various surficial geologic maps covering the Lake Mathews area, and between some of these maps and the surficial geology of the LMSB No. 4 site as observed by the PEAI paleontologic construction monitors. Proctor (1961) mapped subsurface occurrences of the LMF and the Cajalco Pluton on the basis of his studies of bore logs and trench walls that were conducted in support of the enlargement of Mathews Dam and Lake Mathews. However, unlike Morton and Weber (2001) and Morton (2004), surficial geologic mapping by Rogers (1965) and Woodford et al. (1971) reproduced the subsurface geologic mapping by Proctor (1961) but did not map the overlying surficial cover of alluvial fan deposits (Woodford et al., 1971). Instead, the Cajalco Pluton and the LMF are portrayed by Rogers (1965) and Woodford et al. (1971) as geographically widely exposed. A copy of the U.S. Geological Survey (USGS) Steele Peak 7.5-Minute Quadrangle archived at the California Geological Survey (CGS) was annotated by T.H. Rogers when compiling the surficial geologic map of the USGS Santa Ana Sheet (Rogers, 1965). This annotated map indicates clearly that the LMF represents a buried channel deposit. As mapped by Rogers (1965), the deposit parallels Cajalco Road, beginning at the apex of the major curve in the road south of Lake Mathews (Fig. 1) and extending eastward for a distance of approximately 13 km into Mead Valley. However, as mapped by Morton (2001, 2004) and Morton and Weber (2001), the LMF is exposed as 1) two comparatively small isolated remnants lying on the flat just north of the eastern end of Lake Mathews, 2) a comparatively large remnant resting on the flat just south of the western half of Lake Mathews and south of the flat on the adjacent divide north of Dawson Canyon, and 3) two comparatively small remnants that lie up to 5 km south–southwest of Lake Mathews Dam and occur on the drainage divides between Olsen and Dawson Canyons.

PREVIOUS PALEONTOLOGIC INVESTIGATIONS OF THE LAKE MATHEWS FORMATION

Fossilized bones and teeth representing several extinct large-bodied land mammal taxa (felid, medium-sized tapirlike ticholeptine oreodontid, and medium-sized and large camelids) were recovered in 1960 and 1961 at two fossil localities in the borrow areas that provided the fill used in the enlargement of Mathews Dam (Fig. 1; Proctor, 1961, 1962, 1966; Proctor and Downs, 1963; Rogers, 1965; Morton and Gray, 1971; Woodford et al., 1971; Lander, 1977, 1998, 2004; Morton and Matti, 1989; Morton, 2004). These taxa compose the Cajalco Fauna of Lander (1977, 2004). The oreodontid and some of the camelid remains were recovered north of Cajalco Road in Borrow Area "C" (Proctor, 1961; Lander, 2004; Tertiary mammal locality CC34 of Janis et al., 1998, and Lander, 1998), which now is submerged beneath Lake Mathews (Fig. 1). The taxa represented by the fossil remains from this locality comprise the Cajalco Local Fauna (LF, s.s.; Janis et al., 1998; Lander, 1998) of the Cajalco Fauna. The camelid remains include LACM 4184 (ulnar and astragalar fragments) (Lander, 2004). The oreodontid specimen is discussed under "Systematic Paleontology."

Additional LACM camelid specimens (4183, phalanx; 44886, right m2; 150068, partial cervical vertebra; 150069, distal humerus; 150070, distal femur; 150071, proximal left metacarpal; 150072, left astragalus; 150073, distal left tibia; 150074, distal right tibia; 150075, proximal phalanx), as well as a felid specimen (LACM 150067, right medial phalanx), were recovered in Borrow Area "C" and/or south of Cajalco Road in Borrow Area "D" (Fig. 1; Lander, 2004). Only uncatalogued fragments of a camelid limb bone are definitely recorded from Borrow Area "D" (Lander, 2004). The taxon or taxa represented by the remains from the latter locality constitute an unnamed local fauna of the Cajalco Fauna (Lander, 2004). The fossil localities in Borrow Area "C" and Borrow Area "D" both were catalogued subsequently as LACM locality 1541 (Proctor, 1961). Lander and Whistler (2002) assigned the fossil land mammal assemblages from the borrow areas to the Cajalco LF.

Other camelid remains were recovered south of Cajalco Road at Department of Geological Sciences, University of California, Riverside, California (UCR = UCMP), locality RV-7201, either in Borrow Area "D" or at another fossil locality probably less than 1.1 km to the east (Lander, 2004). However, the latter locality is in an area underlain almost entirely by early late Cretaceous monzogranite, with only a very small portion of the area being underlain by axial valley floor deposits of late Pleistocene and Holocene age (Morton and Weber, 2001). This information suggests that UCR locality RV-7201 probably is in Borrow Area "D" and very near, if not the same as, LACM locality 1541. Therefore, the assemblage from UCR locality RV-7201 also is assigned to the unnamed local fauna. Lander (1977) erroneously considered the oreodontid specimen to be from UCR locality RV-7201 and, as a result, based the Cajalco Fauna on the assemblage from this locality. The camelid remains from UCR locality RV-7201 include UCR 14891 (= UCMP 314891, distal metapodial), 14892 (= UCMP 314892, metapodial), and 14893 (= UCMP 314893, right maxilla and associated cranial fragments) (Lander, 2004).

Janis et al. (1998) and Lander and Whistler (2002) did not restrict the Cajalco LF to the

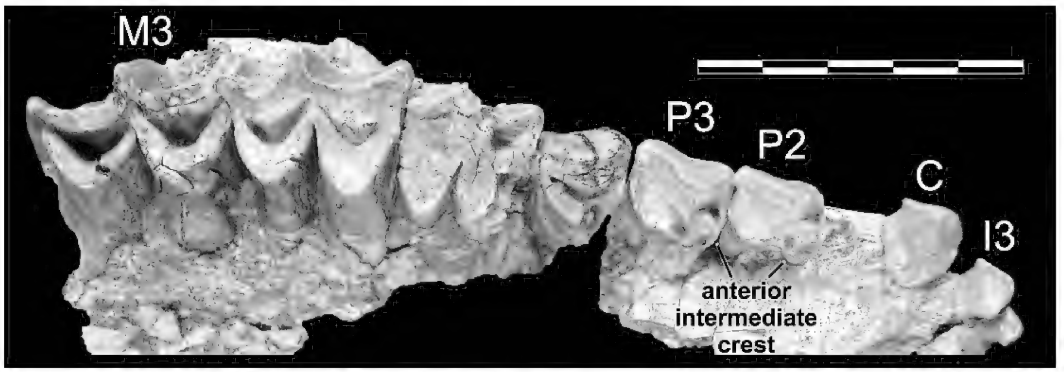

Figure 3 *Merychyus medius compressidens*, Borrow Area "C" LF of Cajalco Fauna, Lake Mathews Formation, LACM locality 1541, California; partial right premaxilla and maxilla with I2-C, P1 alveoli, and P2–M3, LACM 44887, occlusal view. Scale bar = 5 cm.

assemblage from Borrow Area "C" at LACM locality 1541. As a result, it is possible that the local fauna, as they recognized it, also included the assemblages from Borrow Area "D" at LACM locality 1541 and UCR locality RV-7201. Consequently, the Cajalco LF might have represented assemblages from widely separated stratigraphic levels and, therefore, of widely differing geologic ages. For these reasons, Lander (2004) replaced the name Cajalco LF with Borrow Area "C" LF, and applied the latter name only to the assemblage from LACM locality 1541 in Borrow Area "C" (Fig. 1).

During 2000, identifiable tooth fragments representing five genera, three of which are extinct, and five or six extinct species of small-bodied land mammals were recovered from the LMF at PEAI Cajalco Creek locality 1 in the excavation for LMSB No. 4, which lies approximately 2.6 km east–southeast of the Borrow Area "C" fossil locality and 3.1 km east of the fossil locality in Borrow Area "D" (Fig. 1; Lander and Whistler, 2002). The taxa represented by these remains include the small rabbit *Hypolagus* Dice, 1917 (P3); the ground squirrel *Spermophilus* Cuvier, 1825, or *Ammospermophilus* Merriam, 1892 (M3, Mx); possibly the pocket mouse *Perognathus* Maximilian, 1839 (I1); the gopher *Pliosaccomys* (Mx); and the deer mouse *C. esmeraldensis* and/or *C. russelli* (two m2s) (Lander and Whistler, 2002; Lander, 2004). Also recovered was a tooth fragment of an otherwise unidentifiable artiodactyl (Lander and Whistler, 2002; Lander, 2004). These taxa compose the LMSB No. 4 LF of the Cajalco Fauna (Lander and Whistler, 2002; Lander, 2004), which, relying on the overlapping temporal ranges of *Pliosaccomys*, *C. esmeraldensis*, and *C. russelli*, was regarded as late Clarendonian or even earliest? Hemphillian in age by Lander and Whistler (2002). On the other hand, Lander (2004) considered the LMSB No. 4 LF to be early Barstovian to latest Clarendonian, or late Barstovian to early late Hemphillian, in age, depending on which one of the two species of *Copemys* Wood, 1936, was present in the assemblage.

More recently, the San Bernardino County Museum Division of Geological Sciences, Redlands, California, collected additional, as yet unstudied fossilized bones and teeth representing large-bodied land mammal species, including a camelid, from the LMF (Scott and Springer, 2003). These remains were recovered at fossil localities exposed during the drawdown of Lake Mathews from 2001 to 2003.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Superorder Cetartiodactyla Montgelard et al., 1997

Order Artiodactyla Owen, 1848

Suborder Suiformes Jaeckel, 1911, or Tylopoda Illiger, 1811

Infraorder Artionychia Osborn and Wortman, 1893, new rank

Superfamily Oreodontoidea Gill, 1872

Family Oreodontidae Leidy, 1869

Subfamily Ticholeptinae Schultz and Falkenbach, 1940 (nom. nud.), 1941

Genus *Merychyus* Leidy, 1859

Merychyus medius compressidens (Douglass, 1899 [nom. nud.], 1901)
Figures 3 and 4; Table 1

Ustatochoerus cf. *U. californicus* (Merriam) Proctor and Downs (1963:59), Woodford et al. (1971:3427), and Morton and Matti (1989:75).

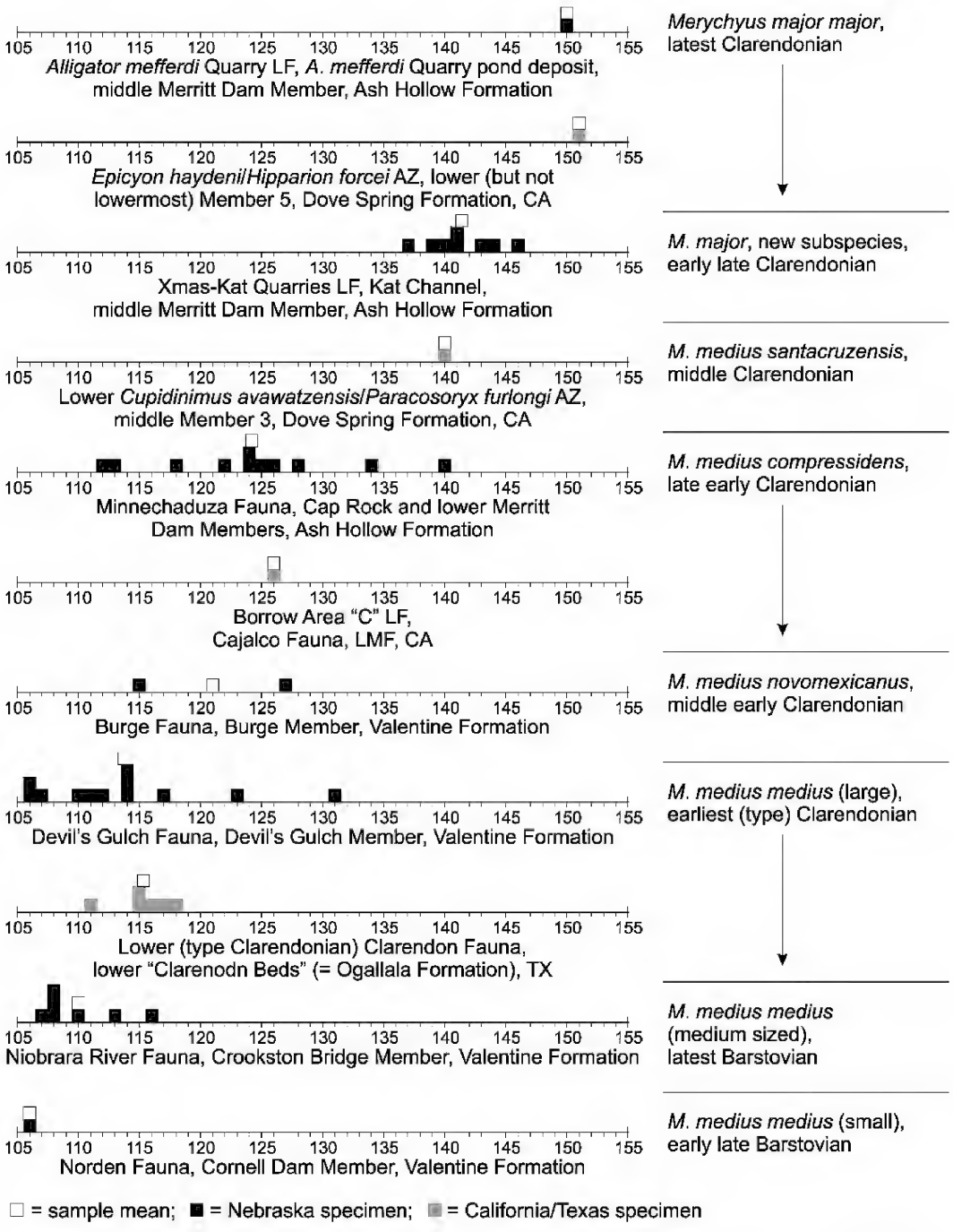
105 110 115 120 125 130 135 140 145 150 155
Alligator mefferdi Quarry LF, A. mefferdi Quarry pond deposit, middle Merritt Dam Member, Ash Hollow Formation
Epicyon haydeni/Hipparion forcei AZ, lower (but not lowermost) Member 5, Dove Spring Formation, CA
Xmas-Kat Quarries LF, Kat Channel, middle Merritt Dam Member, Ash Hollow Formation
Lower Cupidinimus avawatzensis/Paracosoryx furlongi AZ, middle Member 3, Dove Spring Formation, CA
Minnechaduza Fauna, Cap Rock and lower Merritt Dam Members, Ash Hollow Formation
Borrow Area "C" LF, Cajalco Fauna, LMF, CA
Burge Fauna, Burge Member, Valentine Formation
Devil's Gulch Fauna, Devil's Gulch Member, Valentine Formation
Lower (type Clarendonian) Clarendon Fauna, lower "Clarenodn Beds" (= Ogallala Formation), TX
Niobrara River Fauna, Crookston Bridge Member, Valentine Formation
Norden Fauna, Cornell Dam Member, Valentine Formation
Merychyus major major, latest Clarendonian
M. major, new subspecies, early late Clarendonian
M. medius santacruzensis, middle Clarendonian
M. medius compressidens, late early Clarendonian
M. medius novomexicanus, middle early Clarendonian
M. medius medius (large), earliest (type) Clarendonian
M. medius medius (medium sized), latest Barstovian
M. medius medius (small), early late Barstovian
□ = sample mean; ■ = Nebraska specimen; ■ = California/Texas specimen

Figure 4 Histograms showing progressive increase in P1–M3 length between stratigraphically superposed specimens and samples of *Merychyus medius* and *M. major* from strata of early late Barstovian to latest Clarendonian age in Valentine and Ash Hollow formations of north-central Nebraska and adjacent south-central South Dakota, and Dove Spring Formation of Southern California. Specimens from LMF of Southern California and lower part of "Clarendon Beds" of Texas Panhandle shown for comparison. Corresponding specimen and sample data provided in Table 1.

Table 1 Mean P1–M3 lengths for stratigraphically superposed specimens and samples of *Merychyus medius* and *M. major* from strata of early late Barstovian to latest Clarendonian age in Valentine and Ash Hollow formations of north-central Nebraska and adjacent south-central South Dakota, Ogallala Formation of northwestern Kansas, Pawnee Creek Formation of northeastern Colorado, Pojoaque Member of north-central New Mexico, "Clarendon Beds" of Texas Panhandle, Orinda Formation of central California, and Dove Spring and Lake Mathews formations of Southern California. Corresponding individual specimen data for most samples graphed in Figure 4. **ABBREVIATIONS: a** = approximate; **Fm.** = Formation; **Mbr.** = Member.

Stratigraphic unit (land mammal assemblage)	P1–M3 length (mm) Mean	O.R.	n	Taxon
NEBRASKA, SOUTH DAKOTA				
Ogallala Group				
Ash Hollow Fm.				
Merritt Dam Mbr., middle part				
Alligator mefferdi Quarry pond deposit	150.00	150	1	*Merychyus major major*
Kat Channel (Xmas–Kat Quarries LF)	141.38	137–146	8	*M. major*, subsp. nov. (large)
Merritt Dam (lower part) and Cap Rock mbrs. (Minnechaduza Fauna)	124.18	112–140	11	*M. medius compressidens* (includes *Ustatochoerus skinneri*)
Valentine Fm.				
Burge Mbr. (Burge Fauna)	121.00	115–127	2	*M. medius novomexicanus*
Devil's Gulch Mbr. (Devil's Gulch Fauna)	113.75	106–131	12	*M. medius medius* (large)
Crookston Bridge Mbr. (Niobrara River Fauna)	110.00	107–116	7	*M. medius medius* (medium sized)
Cornell Dam Mbr. (Norden Fauna)	106.00	106	1	*M. medius medius* (small)
KANSAS				
Ogallala Fm., Valentine Mbr. (Densmore S LF)	108.00	108	1	*M. medius? schrammi*
COLORADO				
Ogallala Group, Pawnee Creek Fm., upper part (Keota Fauna)	111.00	107–115	3	*M. medius? schrammi*
NEW MEXICO				
Santa Fe Group, Tesuque Fm., Pojoaque Mbr.				
Upper (but not uppermost) part	147.00	147	1	*M. major*, subsp. nov. (large) (*U. skinneri santacruzensis* topotype)
Upper (but not uppermost) part	140.00	140	1	*M. medius santacruzensis* (type)
Lower variegated facies and lower part, middle tuffaceous facies	121.83	114–129	6	*M. medius novomexicanus* (includes *U. profectus espanolensis*)
TEXAS				
"Clarendon Beds" (= Ogallala Fm.), lower part (Lower [type Clarendonian] Clarendon Fauna)	115.33	111–118	6	*M. medius medius* (large)
CALIFORNIA				
Ricardo Group, Dove Spring Fm.				
Mbr. 5, lower (but not lowermost) part (*Epicyon haydeni*/*Hipparion forcei* AZ)	151.00	151	1	*M. major major* (*U. californicus* topotype)
Mbr. 3, lower middle part (Lower *Cupidinimus avawatzensis*/*Paracosoryx furlongi* AZ)	140.00	140a	1	*M. medius santacruzensis?*
Contra Costa Group, Orinda Fm. (Lafayette Ridge LF)	150.00	150a	1	*M. major major*
Lake Mathews Fm. (Borrow Area "C" LF)	126.00	126	1	*M. medius compressidens*

Ustattochoeerus [*sic*] cf. *U. californicus* (Merriam) Morton (1999:14, 2004:16).

Merychyus medius compressidens (Douglass) Lander (2004:5, 2005a:5, 2005b:29).

REFERRED SPECIMEN. LACM 44887, partial right premaxilla and maxilla with I1 alveolus, I2-C, P1 alveoli, and P2–M3 (Fig. 3); partial left premaxilla and maxilla with I1 alveolus, I2-C, and P1–2 roots; and M2–3.

LOCALITY, HORIZON, FAUNAL ASSEMBLAGE, AND AGE. LACM locality 1541, LMF, Borrow Area "C" LF of Cajalco Fauna, late early Clarendonian NALMA (late middle Miocene).

DESCRIPTION. On the basis partly of its P1–M3 length, LACM 44887 represents a medium-sized ticholeptine oreodontid comparable in body size to late early Clarendonian *M. medius compressidens* and earliest Hemphillian *Merychyus major*? *profectus* (Matthew and Cook, 1909), but larger than earlier (early Barstovian to middle early Clarendonian) subspecies of *M. medius* (*Merychyus medius*? *schrammi* [Schultz and Falkenbach, 1941], *Merychyus medius medius*, and *Merychyus medius novomexicanus* Frick, 1929 [nom. nud.] and [Thorpe, 1937, in part]); smaller than the latest subspecies of *M. medius* (middle Clarendonian *Merychyus medius santacruzensis* [Schultz and Falkenbach, 1941]) and the remaining subspecies of *M. major* (early late Clarendonian *M. major*, subsp. nov.; latest Clarendonian *Merychyus major major*; and late early to early late Hemphillian *M. major*?, subsp. nov.); and substantially larger than earlier (latest Arikareean and Hemingfordian) and more primitive species of the genus, including late Hemingfordian *Merychyus relictus* Matthew and Cook, 1909 (Fig. 4, Table 1). The external narial opening of LACM 44887 is damaged but was at least as retracted as in *M. medius* and more retracted than in earlier and more primitive species of the genus. The P2–3 anterior intermediate crest of LACM 44887 forms a large distinct cusp at the anteromedial corner of each tooth, as in virtually every individual of *M. medius* and *M. major*, but only about two thirds of the examples of *M. relictus* (crest still continuous with parametacone in approximately one third of *M. relictus* specimens, all individuals of even earlier and more primitive species of the genus, and all other ticholeptines, but possibly in only one recorded example of *M. medius*) (Fig. 3).

DISCUSSION. On the basis of 1960 and 1961 personal communications from T. Downs, then of the LACM, Proctor (1961) originally assigned the oreodontid specimen (LACM 44887; Fig. 3) from the LMF to the comparatively large-bodied, derived, and tapirlike oreodontid genus *Ustatochoerus* Schultz and Falkenbach, 1941. *Ustatochoerus*, a member of the Ticholeptinae Schultz and Falkenbach, 1940 (nom. nud.) and 1941, was considered no younger than Clarendonian in age (Proctor, 1961). LACM 44887 later was assigned to the very large-bodied, latest Clarendonian species *Ustatochoerus* cf. *U. californicus* (Merriam, 1917 [nom. nud.], 1919) by Proctor and Downs (1963), Woodford et al. (1971), Morton and Matti (1989), and Morton (1999, 2004). These latter workers all regarded the record as Clarendonian or (Woodford et al., 1971) late Clarendonian in age.

However, because Schultz and Falkenbach (1941, 1968:charts 14 and 18a) incorrectly derived *Ustatochoerus* from the late Hemingfordian *Ticholeptus* Cope, 1878, Lander (1977) rejected *Ustatochoerus* and, except for early Barstovian *Ustatochoerus medius mohavensis* Schultz and Falkenbach, 1941, referred all of its subordinate taxa and their respective specimens to *Ticholeptus*. *Ustatochoerus medius mohavensis*, on the other hand, was assigned to *Mediochoerus* Schultz and Falkenbach, 1941, by Lander (1977, 1985, 1998) on the basis of 1973 written and verbal communications, respectively, from M.F. Skinner and R.H. Tedford, then of the DVP, and by all subsequent workers. Correspondingly, Lander (1977) assigned LACM 44887 and the oreodontid in the early Clarendonian (Tedford et al., 1987; Janis et al., 1998) Minnechaduza Fauna to *Ticholeptus compressidens* (Douglass, 1899 [nom. nud.], 1901), one of a number of taxa that Schultz and Falkenbach (1941) had assigned to *Ustatochoerus*. Like the holotypic specimen of *Ustatochoerus compressidens* (Douglass, 1899 [nom. nud.], 1901), LACM 44887 and the oreodontid in the Minnechaduza Fauna represent medium-sized ticholeptine individuals. The *U. compressidens* holotypic specimen (CMNH 801, partial left dentary with c–m3) is from the early Clarendonian (Janis et al., 1998), upper part of the Madison Valley Beds (?= Sixmile Creek Formation) in the Bozeman Group of Gallatin County, southwestern Montana (Lander, 1998). The Minnechaduza Fauna occurs in the Cap Rock Member (Skinner and Johnson, 1984; Tedford et al., 1987, 2004) and the lower part of the overlying Merritt Dam Member in the lower part of the Ash Hollow Formation in the Ogallala Group of north-central Nebraska and adjacent south-central South Dakota (Lander, 2005a).

Subsequently, Lander (1985, 1998) again rejected *Ustatochoerus* and, except for *U. medius mohavensis* and the smaller bodied *Ustatochoerus*? *schrammi* Schultz and Falkenbach, 1941, derived its subordinate taxa from the substantially smaller bodied, late Hemingfordian *M. relictus* instead of *Ticholeptus*. In the subordinate taxa, the anterior intermediate crest of the P1–3 forms a prominent cusp at the anteromedial corner of each tooth, as in the very small-bodied *M. relictus*, but unlike *Ticholeptus* (Schultz and Falkenbach, 1941:fig. 17c–e; 1947:fig. 8; Lander, 1985, 1998). This cusp is developed similarly in LACM 44887 (Fig. 3; Lander, 2004), as in virtually all other early Barstovian to late early Hemphillian examples of *M. medius* and *M. major* and in about two thirds of the specimens of *M. relictus*, the immediate ancestor of *M. medius* according to Lander (1985, 1998).

Consequently, Lander (1985, questionably, 1998) returned *Ustatochoerus medius* (Leidy, 1859), *Ustatochoerus medius novomexicanus* (Frick, 1929 [nom. nud.] and [Thorpe, 1937, in part]), *Ustatochoerus major* (Leidy, 1859), and *Ustatochoerus profectus* (Matthew and Cook, 1909) (genotypic species) to *Merychyus*, where they all were assigned originally. Similarly, the remainder of the taxa (except *U.*? *schrammi* and

U. medius mohavensis) that had been included in *Ustatochoerus* by Schultz and Falkenbach (1941, 1968) also were referred to *Merychyus* by Lander (1998), who synonymized most of the latter species and subspecies on the basis of priority and their similar cranial and dental morphologies and cheek-toothrow lengths. As a result, Lander (1998) recognized only *M. medius medius*, *M. medius novomexicanus*, and *M. major*. For example, Lander (1998) referred *U. compressidens* and LACM 44887 to *M. medius novomexicanus*, as did Lander and Whistler (2002). Thorpe (1937) and Schultz and Falkenbach (1941) designated a dentary (F:AM 32051) representing another medium-sized individual as the *M. medius novomexicanus* colectotypic and lectotypic specimen, respectively. The *M. medius novomexicanus* type locality is in the Pojoaque Member of the Tesuque Formation in the Santa Fe Group of Santa Fe County in north-central New Mexico (Galusha and Blick, 1971). More recently, Lander (2004, 2005a, 2005b) resurrected *U. compressidens* for one of the comparatively larger forms of *M. medius*, and *U. profectus* questionably as the smallest form of *M. major*. LACM 44887 was regarded as referable either to *M. medius compressidens* or to *M. major? profectus* on the basis of size, as reflected by its P1–M3 length, and either late early Clarendonian or earliest Hemphillian in age, respectively (Lander, 2004).

Continuing a trend that began in the late Arikareean, *Merychyus* underwent a progressive increase in average adult body size from the late Barstovian to the latest Clarendonian NALMAs, as documented by a corresponding increase in the mean P1–M3 length in a sequence of stratigraphically superposed samples from the Cornell Dam, Crookston Bridge, Devil's Gulch, and Burge members of the Valentine Formation and from the overlying Cap Rock Member to the middle part of the Merritt Dam Member in the lower and middle parts of the Ash Hollow Formation in the Ogallala Group of north-central Nebraska and adjacent south-central South Dakota (Fig. 4, Table 1; Schultz and Falkenbach, 1941, 1968:chart 18a; Skinner et al., 1968; Lander, 1977, 2005a; Skinner and Johnson, 1984). This increase in body size also is documented stratigraphically from the upper part of Member 2 to the middle part of Member 4 or the lower part of Member 5 of the DSF in the Ricardo Group of the western Mojave Desert in Kern County, Southern California (Fig. 4, Table 1; Lander, 1977, 2005a; Whistler, 1991; Whistler and Burbank, 1992:figs. 4 and 5; Tedford et al., 1987, 2004).

Merychyus also underwent an increase in the degree of retraction of its external narial opening during this same time interval, a change reflecting the development of a short tapirlike proboscis and manifested by the accompanying comparative shortening of the nasals and the dorsal border of the maxilla (Schultz and Falkenbach, 1941, 1968:chart 18a; Lander, 1977, 1998; Prothero and Schoch, 2002). Pronounced discontinuities are observed between the mean P1–M3 lengths and the degrees of retraction of the external narial openings of the earlier (early late Barstovian to late early Clarendonian; smaller, less derived) forms of *Merychyus* from the Cornell Dam Member to the lower part of the Merritt Dam Member on one hand, and the later (early late Clarendonian; larger, more derived) forms of the genus from the middle part of the Merritt Dam Member on the other. On the basis of these discontinuities, only two post-Hemingfordian species of the genus, *M. medius* and *M. major*, respectively, are recognized, whereas less pronounced discontinuities in size separate subspecies within each of these species (Fig. 4, Table 1; Lander, 1998, 2004, 2005a, 2005b).

Reversing the trend of increasing body size, *M. major* subsequently decreased in average adult body size from the latest Clarendonian to the earliest Hemphillian NALMAs, as documented stratigraphically in the lower part of Member 6 of the DSF (Lander, 2005a), in the lower part of the Orinda Formation in the Contra Costa Group of the San Francisco Bay area in central California, and (Skinner et al., 1977; Tabrum, 1981; Lander, 2005a) possibly from the Murphy Member to the Laucomer Member of the Snake Creek Formation in the Ogallala Group of the Nebraska Panhandle in Sioux County. Later in the early Hemphillian NALMA, *M. major* increased in body size again, as documented stratigraphically from the Laucomer Member to the lower part of the Johnson Member in the Snake Creek Formation, and is last recorded in early late Hemphillian strata in the upper part of the Johnson Member (Skinner et al., 1977; Tabrum, 1981; Lander, 2005a). The latter record represents the last record of an oreodontoid.

Edwards (1976, 1982), Tedford et al. (1987), Whistler (1991), and Whistler and Burbank (1992:fig. 4) incorrectly referred the oreodontid specimens from Member 2 of the DSF to *U. profectus* or *U.* cf. *U. profectus*. Lander (1977) and Edwards (1982) mistakenly considered LACM 29771 (left maxillary fragment with P3–M3) to be from Member 3 (= Member 4 of Dibblee, 1952). *Ustatochoerus profectus* is one of the taxa that was used by Whistler and Burbank (1992:figs. 4 and 5) to define the late Barstovian *U. profectus/C. russelli* Assemblage Zone (AZ). Earlier, the specimens from Member 2 had been assigned to *Ustatochoerus* cf. *U. medius* by Woodburne (1971). Later, however, Lander (1998) referred these specimens (LACM 29771, 148194, and 149293 from LACM localities 1108, 6620, and 4704, respectively, and probably UCMP 27123 and 27124 from an undetermined

stratigraphic interval in the DSF at UCMP locality V-65199) to *Merychyus medius novomexicanus*, whereas Lander and Whistler (2002) and Tedford et al. (2004) referred them to *M. medius medius* and *U. medius*, respectively. More recently, Lander (2005a, 2005b), reassigned the specimens to the slightly larger bodied *M. medius compressidens*, one of the largest bodied subspecies of *M. medius* (Fig. 4, Table 1). LACM locality 6620 is the first fossil occurrence shown above the basal conglomerate (Member 1) of the DSF by Whistler and Burbank (1992:fig. 3, section D) (D.P. Whistler, written communication, 2005). Consequently, LACM 148194 (right dentary fragments with p1–3 roots and m2, left dentary fragment with m2, and fragment of left p4) is from much lower in Member 2 and the *U. profectus/C. russelli* AZ than shown by Whistler and Burbank (1992:figs. 4 and 5) and probably from about the same level as the first local appearance of *C. russelli*. Therefore, LACM 148194 represents the earliest documented record of the species from California. As shown by Whistler and Burbank (1992:fig. 4) and contrary to Tedford et al. (2004), the lowest local occurrence of *Copemys*, *C. russelli* and/or *Copemys* cf. *C. longidens* (Hall, 1930), is from just above, rather than in, the basal conglomerate.

Merychyus medius compressidens also occurs in the early Clarendonian Minnechaduza Fauna from the lower part of the Ash Hollow Formation and includes the holotypic and topotypic specimens of *Ustatochoerus skinneri* Schultz and Falkenbach, 1941, from the same stratigraphic interval (Fig. 2; Lander, 1977, 1998, 2004, 2005a, 2005b). Schultz and Falkenbach (1941) assigned most of the sample from the lower part of the Ash Hollow Formation erroneously to *U. profectus*, as noted first by Tabrum (1981), whereas Lander (1998) and Lander and Whistler (2002) assigned the entire sample to *M. medius novomexicanus*.

The Minnechaduza Fauna was founded on the fossil land mammal assemblage from UCMP locality V-3326 (Little Beaver B Quarry), which Skinner and Johnson (1984) considered to be in the Cap Rock Member of the Ash Hollow Formation. Webb (1969), Skinner and Johnson (1984), and Tedford et al. (1987, 2004) restricted the Minnechaduza Fauna to assemblages from the Cap Rock Member. However, because the *M. medius compressidens* sample from the lower part of the Ash Hollow Formation includes examples from both the Cap Rock Member and the lower part of the Merritt Dam Member, the Minnechaduza Fauna was extended stratigraphically upward by Lander (2005a) to include the assemblages from the lower part of the Merritt Dam Member as well. Moreover, although shown as occurring in the Cap Rock Member by Skinner and Johnson (1984:fig. 33, section 31, quarry 58), UCMP locality V-3326 is shown lying above the "lower Cap Rock" bed by Webb (1969:fig. 4). Furthermore, this locality, only 4.6 m below the top of a bluish gray volcanic ash bed (= Davis Ash; Skinner and Johnson, 1984), probably is from a stratigraphic level above that of UCMP locality V-6257 (Above Burge B), which lies 6.7 m below the top of the bluish gray ash layer (Webb, 1969) and was regarded as being near the base of the Merritt Dam Member by Skinner and Johnson (1984). For these reasons, UCMP locality V-3326 also is considered to be near the base of the Merritt Dam Member, which, in turn, is regarded as the source of the type assemblage for the Minnechaduza Fauna, not the Cap Rock Member. According to Webb (1969:fig. 4) and as illustrated by Skinner and Johnson (1984:figs. 15, 33, 38, section 31, quarry 58, sections 57, 67, 68), the Davis Ash, which lies approximately 15 m above the local base of the Merritt Dam Member (Skinner and Johnson, 1984), fills channels that have incised into underlying strata that include the lowermost part of the Merritt Dam Member and UCMP locality V-3326 (Skinner and Johnson, 1984:fig. 38, section 31). For this reason, the channels containing the Davis Ash are considered to be at the local base of the middle part of the Merritt Dam Member. The Davis Ash has been determined to be 11.55 ± 0.12 Ma in age on the basis of a K-Ar radiometric dating analysis, whereas the Swallow Ash, which lies 1 m above the local base of the Cap Rock Member (Skinner and Johnson, 1984), has been determined to be 12.18 ± 0.12 Ma old on the basis of a similar analysis (Fig. 2; Swisher, 1992; Tedford et al. 2004).

Relying on measurements provided by Schultz and Falkenbach (1941:tables 1, 9), the p1–4 length (52.5 mm) of the *M. medius compressidens* holotypic specimen (CMNH 801) is near the middle of the observed range (O.R.) of this parameter for the combined samples from the lower part of the Ash Hollow Formation that they assigned to *U. profectus* and *U. skinneri*. On the other hand, the mean P1–M3 length for the topotypic specimens of *M. medius novomexicanus* from the Pojoaque Member of New Mexico, although only 1.9% less than the mean of this parameter for the sample from the lower part of the Ash Hollow Formation, is only 0.7% greater than the mean for the sample from the Burge Member of the Valentine Formation (Fig. 4, Table 1). Following Lander (1977, 1998), the *M. medius novomexicanus* topotypic specimens include the holotypic and topotypic specimens of *Ustatochoerus profectus espanolensis* Schultz and Falkenbach, 1941, on the basis of similarities in their P1–M3 lengths and the degree of retraction of their external narial openings. The Burge Member sample is assigned to *M. medius novomexicanus* because, like the Pojoaque Member sample, it appears to represent a slightly smaller form than that from the lower part of the

Ash Hollow Formation on the basis of its mean P1–M3 length (Fig. 4, Table 1). Moreover, the external narial openings are at least slightly less retracted in the samples from the Burge and Pojoaque members than in the sample from the lower part of the Ash Hollow Formation.

In this report, contrary to Tedford et al. (1987, 2004) and Janis et al. (1998), respectively, the Burge Fauna from the Burge Member is not regarded as latest Barstovian or earliest Clarendonian in age, or coeval with the Barstovian–Clarendonian boundary. The latest Barstovian (Janis et al., 1998; Tedford et al., 2004) Devil's Gulch Fauna from the Devil's Gulch Member, which underlies the Burge Member, contains a comparatively large form of *M. medius medius* (Lander, 2005b). The mean P1–M3 length for the Devil's Gulch Member sample is comparable to that for the oreodontid in the Lower Clarendon Fauna from the lower part of the "Clarendon Beds" (= Ogallala Formation) of Donley County in the Texas Panhandle (Lander, 1985, 2005b), but, like the latter sample, somewhat less than the means of this parameter for the *M. medius novomexicanus* and *M. medius compressidens* samples that compose the Burge and Minnechaduza faunas, respectively (Fig. 4, Table 1). The fossil land mammal assemblages from the "Clarendon Beds" are the basis for the Clarendonian NALMA (Wood et al., 1941). The Lower Clarendon Fauna includes the fossil land mammal assemblages from the F:AM MacAdams Quarry, which is in the lower part of the "Clarendon Beds" (Tedford et al. 1987), and the F:AM Spade Flats locality, which presumably also is in the lower part of the formation.

Again contrary to Tedford et al. (1987, 2004) and Janis et al. (1998), Lander (1977) and Tabrum (1981) considered the Lower Clarendon Fauna to be older than the Minnechaduza Fauna because it contains a smaller form of *U. profectus*, *Ustatochoerus profectus studeri* Schultz and Falkenbach, 1941. Although Schultz and Falkenbach (1941) referred the specimens from the "Clarendon Beds" at MacAdams Quarry and the Spade Flats locality to *U. profectus studeri*, Lander (1985) noted the similarities between the samples from the lower part of the "Clarendon Beds" and the Devil's Gulch Member in terms of their P1–M3 lengths and the degrees of retraction of their external narial openings. Because of these similarities and following Lander (1977), Lander (1985) assigned both samples to *M.? medius*, later (1998, 2005b), assigning them to *M. medius medius*. Consequently, the Devil's Gulch Fauna, following Lander (1985, 2005b), is regarded as a correlative of the Lower Clarendon Fauna and, therefore, earliest Clarendonian in age, the Burge Fauna middle early Clarendonian, and the Minnechaduza Fauna late early Clarendonian (Fig. 2). Schultz (2002) assigned the "Clarendon Beds" sample to *M. novomexicanus*. The holotypic and topotypic specimens of *U. profectus studeri* from the "Coetas" (= Ogallala) Formation of Potter County in the Texas Panhandle, on the other hand, are assignable to *M. medius novomexicanus* according to Lander (1998) on the basis of their mean P1–M3 length (123 mm, O.R. = 119–127 mm, n = 2) and, as in the one specimen from the Burge Member in which this character is observable and in contrast to most examples of *M. medius medius*, the anomalous development of a slightly less retracted external narial opening in the holotypic specimen. The external narial opening is somewhat less retracted in the *U. profectus studeri* holotypic specimen (F:AM 43031) than in any specimen from the "Clarendon Beds," whereas the narial opening in F:AM 37225 from the Burge Member is somewhat less retracted than in any other specimen from the Valentine Formation. Schultz (2002) assigned the "Coetas" Formation sample to *M. novomexicanus*, as well. The *U. profectus studeri* type locality also yielded the Bivins Ranch LF (Fig. 2; Schultz, 2002).

The *Merychyus* samples from Member 2 of the DSF and from the lower part of the Ash Hollow Formation represent a medium-sized form of *Merychyus*, relying on M1–3 lengths provided by Schultz and Falkenbach (1941:table 9) and Lander (2005a), as do the samples from the Valentine Formation on the basis of their P1–M3 lengths (Fig. 4, Table 1). The M1–3 length of LACM 29771 from the DSF at LACM locality 1108 is 74 mm. LACM locality 1108 ("Schultz Bonebed") is recorded as lying just below two 8- to 9-m-thick tuff beds. These tuff units probably represent the pink tuff breccia layers recognized by Whistler (1969, 1991) and shown by Whistler and Burbank (1992:fig. 3, sections A, D–F, fig. 4) as locally composing the lower part of overlying Member 3 of the DSF. LACM locality 1108 is the second fossil occurrence shown below the tuff breccia by Whistler and Burbank (1992:fig. 3, section D) (D.P. Whistler, written communication, 2005). The M1–3 length (69 mm) of another medium-sized individual (UCMP 27124, left maxillary fragment with P4–M3 from UCMP locality V-65199) suggests that this specimen is from Member 2 as well. Unfortunately, UCMP 27124 and a second specimen (UCMP 27123, left dentary fragment with p3–m1) from the same general locality lack stratigraphic data. Although they correspond to individuals similar in size to that represented by LACM 29771, both specimens also correspond to individuals similar in size to that represented by LACM 146098 from overlying Member 6 of the DSF. Specimens UCMP 27124 and 27123 were collected by A.M. Alexander and L. Kellogg in 1924. A review of Alexander's 1924 field notes, which are on file at the UCMP, indicates that they did not prospect

as high in the DSF as Member 6 (D.P. Whistler, written communication, 2005). Therefore, both specimens probably are from Member 2. Partly on the basis of measurements provided by Schultz and Falkenbach (1941:table 9) for the *Merychyus* samples from the Ogallala Group in Nebraska that they assigned to *Ustatochoerus*, the observed range of M1–3 lengths presented by Lander (2005a) for LACM 29771 from Member 2 and UCMP 27124 overlaps the upper part of the observed range of this parameter for the *U. medius* sample from that part of the Valentine Formation lying below the Burge Member that Lander (1998) assigned to *M. medius medius*, overlaps the lower part of the corresponding observed range for the *M. medius novomexicanus* sample from the Burge Member (mean = 75 mm, O.R. = 73–77 mm, n = 2 on the basis of F:AM 39225 and 104884), but is within the observed range of the parameter for the combined *U. profectus–U. skinneri* sample from the lower part of the Ash Hollow Formation that Lander (2004, 2005a, 2005b) assigned to *M. medius compressidens*. On the other hand, and again on the basis of measurements provided by Schultz and Falkenbach (1941:table 9), the M1–3 length for LACM 29771 also is very near the mean and the middle of the observed range of this parameter for the *M. medius novomexicanus* sample from the Burge Member and near the middle of the observed range of the parameter for the *M. medius compressidens* sample from the lower part of the Ash Hollow Formation. Because of the reidentification of the specimens from Member 2, Lander and Whistler (2002) correspondingly renamed the *U. profectus/C. russelli* AZ the *M. medius medius/C. russelli* AZ, whereas Lander (2005a, 2005b) referred to this zone as the *M. medius/C. russelli* AZ (Fig. 2). Although Tedford et al. (2004) regarded this assemblage zone as a correlative of the Burge Fauna, Whistler and Burbank (1992) considered the *M. medius/C. russelli* AZ a correlative of those faunas in the Valentine Formation that underlie the Burge Fauna. Lander (2005a, 2005b), on the other hand, correlated the lower and middle parts of the assemblage zone in Member 2 with the late early Clarendonian Minnechaduza Fauna. The upper part of the *M. medius/C. russelli* AZ occurs immediately above the tuff breccia unit that locally composes the lower part of Member 3 (Whistler and Burbank, 1992:fig. 4).

A tuff layer that lies 113 m above the base of the DSF in Member 2 (Tedford et al., 2004; M.E. Perkins, written communication, 2006) and yielded sample epb92-40 of Perkins et al. (1998) had been correlated geochemically with Cougar Point Tuff Unit (CPT) V (Perkins et al., 1998:fig. 3; Tedford et al., 2004). CPT V, in turn, occurs in the Tuff of Ibex Peak in the Bruneau–Jarbidge Volcanic Field of the Snake River Plain Volcanic Province at Trapper Creek in southwestern Idaho (Perkins et al., 1995) and has been determined to be 12.071 ± 0.037 and 12.169 ± 0.032 Ma in age on the basis of ^{40}argon/^{39}argon single-crystal laser fusion (Ar/Ar) radiometric dating analyses (Perkins et al., 1998:table 6, samples wjr93-436 and tc89-18a, respectively; Perkins and Nash, 2002; Tedford et al., 2004). Sample epb92-40 almost certainly is from the second tuff unit (Tra-1 of Whistler, 1969) shown lying above the base of the DSF by Whistler and Burbank (1992:fig. 3, sections E and F) (M.E. Perkins, written communication, 2006) and probably is bracketed by LACM localities 6620 and 1108 in section D of Whistler and Burbank (1992:fig. 3) (D.P. Whistler, written communication, 2005). Although shown lying very near the top of the *M. medius/C. russelli* AZ by Tedford et al. (2004:fig. 6.2D), the presumed equivalent of CPT V in the DSF actually lies between the lower and middle parts of the zone. The younger radiometric age determination for CPT V suggests that the *M. medius/C. russelli* AZ is largely correlative with the Minnechaduza Fauna. On the other hand, the older age determination indicates that only the middle and upper parts of the assemblage zone from the upper part of Member 2 and to the lower middle part of Member 3, respectively, correlate with the Minnechaduza Fauna, whereas the lower part of the zone in the lower part of Member 2 probably is a correlative of the Burge Fauna (Fig. 2). However, Perkins and Nash (2002) subsequently considered the tuff unit that yielded sample epb92-40 to be 12.29 ± 0.10 Ma in age by interpolation. Consequently, the equivalency of CPT V and tuff unit Tra-1 is suspect (M.E. Perkins, written communication, 2006).

Whistler and Burbank (1992:fig. 3, section E, and fig. 4) showed *U. californicus* first appearing low in the middle part of Member 3 of the DSF, just above the pink tuff breccia interval that constitutes the lower part of the member, also as shown by Whistler and Burbank (1992:fig. 3, sections A, D, and E). This lowermost local occurrence of *U. californicus*, also reported by Whistler (1991), is one of the taxonomic records used by Whistler and Burbank (1992:figs. 4 and 5) to characterize the lower part of the early Clarendonian *Cupidinimus avawatzensis/Paracosoryx furlongi* AZ in the middle part of Member 3. The *U. californicus* record from the middle part of the member includes LACM 143524 from LACM locality 4847. LACM locality 4847 is the first fossil occurrence shown above the tuff breccia unit by Whistler and Burbank (1992:fig. 3, section E) (D.P. Whistler, written communication, 2005). On the other hand, the highest local occurrence of *C. russelli* and the lowest local occurrence of *Cupidinimus avawatzensis* Barnosky, 1986, are from only a few meters above the same unit at LACM localities 3672 and 4844,

respectively (D.P. Whistler, written communication, 2007) and, following Whistler (1969), presumably are the first fossil occurrence shown above the tuff breccia interval by Whistler and Burbank (1992:fig. 3, section D). Correspondingly, the lowest local occurrence of *U. californicus* at LACM locality 4847 is very near the base of the *C. avawatzensis/P. furlongi* AZ.

The M1–3 length (84 mm) of LACM 143524 is greater than in the specimens from underlying Member 2 and less than those (O.R. = 89–103 mm, on the basis of LACM 4153, LACM 29768, and UCMP 27124) for the latest Clarendonian holotypic and topotypic specimens of *U. californicus* that were shown as having been derived from overlying Member 5 by Whistler and Burbank (1992:fig. 4) but, on the basis of measurements provided by Schultz and Falkenbach (1941:table 9) for the samples from Nebraska that they assigned to *Ustatochoerus*, within (and near middle of) the observed range of M1–3 lengths only for the sample from the Kat Channel in the Merritt Dam Member. Moreover, relying on measurements provided by Lander (2005a) and Schultz and Falkenbach (1941:table 9), the approximate P1–M3 length of LACM 143524 (revised from Lander, 2005a), comparable to that only for the largest individual of *M. medius compressidens* in the sample from the lower part of the Ash Hollow Formation, also is very near the means of this parameter for the Kat Channel sample that they assigned to *U. major*, and for the sample from the Pojoaque Member (Galusha and Blick, 1971) that they assigned to *Ustatochoerus skinneri santacruzensis* Schultz and Falkenbach, 1941 (Fig. 4, Table 1). It should be noted, however, that the observed range (151–162 mm) of P1–M3 lengths for the Kat Channel sample of *U. major* that is listed in table 9 of Schultz and Falkenbach (1941) conflicts with the P1–M3 length (141 mm) for the *U. major* specimen (F:AM 34220) from this sample that is listed in their table 1 and with the observed range (137–146 mm) provided by Lander (2005a) for the same sample. Moreover, the observed range (139–155 mm) of p1–m3 lengths that they (Schultz and Falkenbach, 1941) provided in their table 9 for the same sample appears to be too low when compared with that for the P1–M3. Therefore, it is highly probable that the observed ranges of the P1–M3 and p1–m3 lengths for *U. major* have been transposed in their table 9, although a P1–M3 length of 155 mm still is larger than in any *Merychyus* specimen measured for this study and probably is incorrect. The P1–M3 lengths of the measured specimens comprising the Kat Channel sample are presented in Figure 4.

Schultz and Falkenbach (1968:table 18) assigned the Kat Channel to the middle part of the Ash Hollow Formation. The Kat and Xmas channels are included in the middle part of the Merritt Dam Member in this report because, as illustrated by Skinner and Johnson (1984:fig. 17 and fig. 33, section 33), both channels have incised into underlying strata that include the lowermost part of the Merritt Dam Member.

Skinner and Johnson (1984), on the basis of similarities of the underlying fossil assemblages, concluded that the *Machaerodus* Ash, which immediately overlies the fossil-bearing interval in the Kat and Xmas channels at the F:AM *Leptarctus*, Kat, Line Kat, *Machaerodus*, and Xmas Quarries (Skinner and Johnson, 1984:fig. 17, fig. 33, section 33, and fig. 38, section 65), might be the same as the volcanic ash bed that overlies the fossil-bearing interval in the Merritt Dam Member at the F:AM Wade Quarry. Alroy (2002), on the other hand, suggested that the volcanic ash bed at Wade Quarry, in turn, might be the Davis Ash. These quarries all have yielded remains of a previously undescribed large bodied subspecies of *M. major*. Lander (1998), contrary to Schultz and Falkenbach (1941), assigned the immature individual from Wade Quarry to *M. major*.

Skinner and Johnson (1984) noted that any lithologic difference between the *Machaerodus* and Davis ashes is not discernable. Regrettably, the stratigraphic relations of the *Machaerodus* and Davis ashes have not been determined with certainty. Relying mostly on fission-track radiometric age determinations of glass shards that were provided to them by J.D. Boellstorff (personal communication, 1981), Skinner and Johnson (1984) suggested that the Davis Ash is slightly older than the *Machaerodus* Ash and that the latter ash is in a channel deposit that presumably cuts though underlying strata containing the Davis Ash. Unfortunately, fission-track analyses of glass shards usually are considered comparatively unreliable, unless it has been documented that annealing of the fission tracks in the shards has not occurred or that a correction factor was applied during the analyses (Seward, 1979). Annealing and the subsequent loss of fission tracks result in age determinations that are too young (Seward, 1979). However, as illustrated by Skinner and Johnson (1984:figs. 15–17, 23, 33, 38, section 31 and 33 [quarry 79 Xmas Quarry], section 65 [quarry 76, Wade Quarry], section 66 [quarry 68, Horn Quarry], sections 67 and 68), the *Machaerodus* and Davis ashes both occur low in the Merritt Dam Member but never occur at the same locality in stratigraphic superposition. Moreover, exposures of the *Machaerodus* Ash in the F:AM Wade and Horn Quarries at their (Skinner and Johnson, 1984:figs. 23, 38) sections 65 (quarry 76) and 66 (quarry 68), respectively, are as little as 0.8 km from an exposure of the Davis Ash at their section 67. Furthermore, according to Webb (1969:fig. 4) and as shown by Skinner and Johnson (1984:fig.

33, section 31), the Davis Ash, like the *Machaerodus* Ash, is in a channel that has incised into the lowermost part of the Merritt Dam Member. For these reasons, the *Machaerodus* Ash is considered to be the same as the Davis Ash. Correspondingly, the Xmas–Kat Quarries LF and the new subspecies of *M. major* are slightly older than 11.55 Ma in age (Fig. 2).

Following Lander (1977), Lander (1998) assigned the samples from the middle part of Member 3, the Kat Channel, and the Pojoaque Member to *M. major*. More recently, however, Lander (2005a, 2005b) assigned these samples to *M. major santacruzensis* (Schultz and Falkenbach, 1941) and the early late Clarendonian NALMA because they represent large (but not very large) individuals with highly retracted external narial openings in the Kat Channel sample (F:AM 34220 and 34221) and a topotypic specimen (F:AM 34400) of *M. major santacruzensis*. However, as illustrated by Thorpe (1937:fig. 149) and Schultz and Falkenbach (1941:fig. 10), the *M. major santacruzensis* holotypic specimen (F:AM 32050) probably represents a large-bodied subspecies of *M. medius* because its external narial opening, although incomplete, appears to have been much less retracted than in *M. major* from the Kat Channel and F:AM 34400. Therefore, F:AM 34400 and the Kat Channel sample are retained in *M. major* as a newly recognized, early late Clarendonian subspecies that is slightly smaller bodied than latest Clarendonian *M. major major* but slightly larger bodied than, and with a much more retracted narial opening compared with, *M. medius santacruzensis* (Fig. 4, Table 1). Correspondingly, F:AM 34400 no longer is regarded as a topotypic specimen of *M. medius santacruzensis*.

Unfortunately, the external narial opening is not preserved in LACM 143524 from the DSF. However, the approximate P1–4 length (54 mm) of this specimen is immediately below the observed range of this parameter for the sample from the Kat Channel that Schultz and Falkenbach (1941:table 9) assigned to *U. major* but is the same as the P1–dP4 length of the smaller of two specimens (UCMP 32310) from the Merritt Dam Member in the F:AM Big Spring Canyon Quarries at UCMP locality V-3322 in Bennett County, southwestern South Dakota. Tedford et al. (1987) considered the Big Spring Canyon LF to be intermediate in age between the late early Clarendonian Minnechaduza Fauna and the early late Clarendonian Xmas–Kat Quarries LF from the Kat Channel (Fig. 2). Moreover, the degree of retraction of the external narial opening appears to have been similar in UCMP 32310 and the *M. medius santacruzensis* holotypic specimen (F:AM 32050), as illustrated by Gregory (1942:fig. 17) and Schultz and Falkenbach (1941:fig. 10), respectively, whereas the P1–dP4 length (58.0 mm) of the larger specimen (UCMP 32331) from UCMP locality V-3322 is virtually the same as the P1–4 length for the holotypic specimen (57.5 mm; Schultz and Falkenbach, 1941:table 1). On the basis of measurements provided by Schultz and Falkenbach (1941:table 1), the M1–3 and P1–M3 lengths of the holotypic specimen, in turn, are virtually the same as those for LACM 143524 (Fig. 4, Table 1). Therefore, LACM 143524 and the Big Spring Canyon LF sample are assigned questionably to *M. medius santacruzensis*. Correspondingly, the lower part of the *C. avawatzensis/P. furlongi* AZ and the Big Spring Canyon LF are regarded as middle, rather than early, Clarendonian in age, contrary to Whistler and Burbank (1992:fig. 5) and Tedford et al. (1987), respectively, as is the *M. medius santacruzensis* holotypic specimen (Fig. 2).

LACM locality 4847 lies below the tuff unit (Tra-3 of Whistler, 1969) that lies low in the middle part of Member 3 and has been determined to be 11.8 ± 0.9 Ma in age on the basis of a fission-track radiometric dating analysis (Cox and Diggles, 1986; Loomis and Burbank, 1988; Whistler and Burbank, 1992:fig. 3, sections D–F; Perkins et al., 1998:fig. 3, sample epb92-42; David P. Whistler, written communication, 2005). Tuff unit Tra-3 has been correlated geochemically with the Ibex Peak 8 Ash (= CPT VII), which occurs in the Tuff of Ibex Peak at Trapper Creek in southwestern Idaho and has been determined to be 11.80 ± 0.04 Ma old by extrapolation (Perkins et al., 1998:fig. 3). Another tuff bed in the DSF (sample epb94-580 of Perkins et al., 1998:fig. 3) lies 29 m below a tuff layer questionably identified as the one that yielded sample epb92-42 and 45 m below the equivalent of the Rainier Mesa Ash (sample epb92-46 of Perkins et al., 1998:fig. 3) (M.E. Perkins, personal communication, 2006b). The tuff layer that yielded sample epb92-580 was shown by Perkins et al. (1998:fig. 3) lying just below the equivalent of the Ibex Peak 8 Ash in the DSF and correlated geochemically with the Ibex Hollow Ash in the Tuff of Ibex Peak. The Ibex Hollow Ash, in turn, has been determined to be 11.93 ± 0.03 Ma in age on the basis of an Ar/Ar radiometric dating analysis (Perkins et al., 1995, 1998:fig. 3, sample tc89-21a; Perkins and Nash, 2002). The equivalent of the Ibex Hollow Ash in the DSF possibly is the tuff unit (Tra-2 of Whistler, 1969) shown lying immediately below tuff unit Tra-3 by Whistler and Burbank (1992:fig. 3, sections D–F). Tuff unit Tra-2, like unit Tra-3, also lies above LACM locality 4847 (D.P. Whistler, written communication, 2005; see Whistler and Burbank, 1992:fig. 3, section E). Consequently, LACM 143524 probably is much too old to be assignable to *M. major*, subsp. nov., and, correspondingly, *M. medius santacruzensis* presumably is older than 11.93 Ma in age (Fig. 2).

The approximate P1–4 length (54 mm) of another specimen (UCR 13229 = UCMP 313229, left maxillary fragment with P1 alveoli and P2–broken P4) from the uppermost part of Member 3 (= Member 4 of Dibblee, 1952) at UCR (= UCMP) locality RV-6009 is the same as that for LACM 143524. Unfortunately, as with LACM 143524, the external narial opening is not preserved in this specimen either. UCR locality 6009 occurs about 11 m below the pink tuff breccia layer reported by Dibblee (1952) as lying at the base of the lower basalt unit that comprises the lower part of Member 4 (= Member 5 of Dibblee, 1952). This locality might be the uppermost fossil locality shown by Whistler and Burbank (1992:fig. 3, section D) just below the lower basalt interval and immediately above tuff unit Tra-5 of Whistler (1969), the first tuff bed shown below the basalt unit by Whistler and Burbank (1992:fig. 3 sections D–F).

Perkins et al. (1998:fig. 3, samples epb92-31 and epb82-30, respectively) showed the equivalent of the Coal Valley Ash in the DSF lying below the equivalent of CPT XII, which, in turn, lies very low in the middle part of Member 4, immediately above the lower basalt interval at the base of the member (M.E. Perkins, written communication, 2006). In the DSF, the equivalent of the Coal Valley Ash lies about 34 m above the equivalent of the Rainier Mesa Ash (M.E. Perkins, written communication, 2006), and might be the same as tuff unit Tra-5 of Whistler (1969). The Coal Valley Ash in the Coal Valley Formation of west-central Nevada has been determined to be 11.49 Ma in age on the basis of a K-Ar radiometric dating analysis (Evernden et al. [1964], sample KA-551; converted with the use of revised decay and abundance constants provided by Dalrymple [1979]) and 11.51 ± 0.10 by interpolation (Perkins et al., 1998:fig. 3, sample as89-47). If UCR locality 6009 is above tuff unit Tra-5, then UCR 13229 is slightly younger than 11.51 Ma in age. However, the ranges of the estimated errors for the Coal Valley Ash and the Davis (?= *Machaerodus*) Ash in the Kat Channel of Nebraska overlap substantially, suggesting that the middle part of the *C. avawatzensis/P. furlongi* AZ in the uppermost part of Member 3 of the DSF is an approximate correlative of the Xmas–Kat Quarries LF and early late Clarendonian in age (Fig. 2). Correspondingly, UCR 13229 is assigned questionably to *M. major*, subsp. nov., despite its possibly lesser P1–4 length, which, on the basis of measurements provided by Schultz and Falkenbach (1941:table 9), is at or immediately below the base of the observed range of P1–4 lengths for the Kat Channel sample.

Whistler and Burbank (1992:fig. 5) assigned the *M. medius/C. russelli* and *C. avawatzensis/P. furlongi* AZs to the Cerrotejonian (Mammalian) Stage. However, the *M. medius/C. russelli* AZ and the lower and middle parts of the *C. avawatzensis/P. furlongi* AZ from below the lower basalt unit at the base of Member 4 are below the lowest local occurrences of those taxa whose restricted biostratigraphic ranges were used by Savage (1955) to define the Cerrotejonian Stage. These taxa include the canid *Borophagus littoralis* Vander Hoof, 1931, and the equids *Pliohippus tehonensis* (Merriam, 1915) (?= *Pliohippus fairbanksi* Merriam, 1915, which includes *Pliohippus tantalus* Merriam, 1913, according to MacFadden, 1998) and *Nannippus* (= *Hipparion*) *tehonense* (Merriam, 1916). For this reason, Lander (2005b) considered the record of *M. medius santacruzensis* from the lower part of the *C. avawatzensis/P. furlongi* AZ in the middle part of Member 3, like the records of *M. medius compressidens* from the *M. medius/C. russelli* AZ in underlying Member 2, to be pre-Cerrotejonian in age, contrary to Whistler and Burbank (1992:fig. 4). On the other hand, Tedford et al. (2004) correlated the *M. medius/C. russelli* AZ with the South Tejon Hills LF, which was Savage's (1955) basis for the Cerrotejonian Stage and includes the lowest local occurrence of *H. tehonense* (Figs. 2 and 5). Moreover, *P. tantalus*, which actually has priority over *P. fairbanksi* and, therefore, possibly *P. tehonensis* (contrary to MacFadden, 1998), occurs as low as the *M. medius/C. russelli* AZ in the DSF (Whistler and Burbank, 1992, figs. 4 and 5). Contrary to Savage (1955), however, the South Tejon Hills LF occurs in the continental Bena Conglomerate of the southeastern San Joaquin Valley in Kern County, Southern California, not in the overlying marine "Santa Margarita" Formation (Prothero and Tedford, 2000; Tedford et al., 2004). Presumably, the records of *P. tehonensis* (?= *P. tantalus*) and *H. tehonense* from the Bena Conglomerate are older than the first appearances of these taxa in the DSF, as shown by Whistler and Burbank (1992:fig. 6) (Prothero and Tedford, 2000; Tedford et al., 2004). Regrettably, a magnetostratigraphic zonation of the Bena Conglomerate that would allow its correlation with a restricted stratigraphic interval in the DSF has not been compiled (Prothero and Tedford, 2000; Tedford et al., 2004). Moreover, the reported occurrence of *Ustatochoerus* in the South Tejon Hills LF by Tedford et al. (2004) cannot be verified (R.H. Tedford, written communication, 2006).

In addition to the records from Member 3, Whistler and Burbank (1992:fig. 4) also showed *U. californicus* occurring in the middle part of Member 4 (= Member 5 of Dibblee, 1952) of the DSF (between lower and upper basalt units at bottom and top, respectively, of member; Cerrotejonian upper part of *C. avawatzensis/P. furlongi* AZ), and in overlying Member 5 and the lower

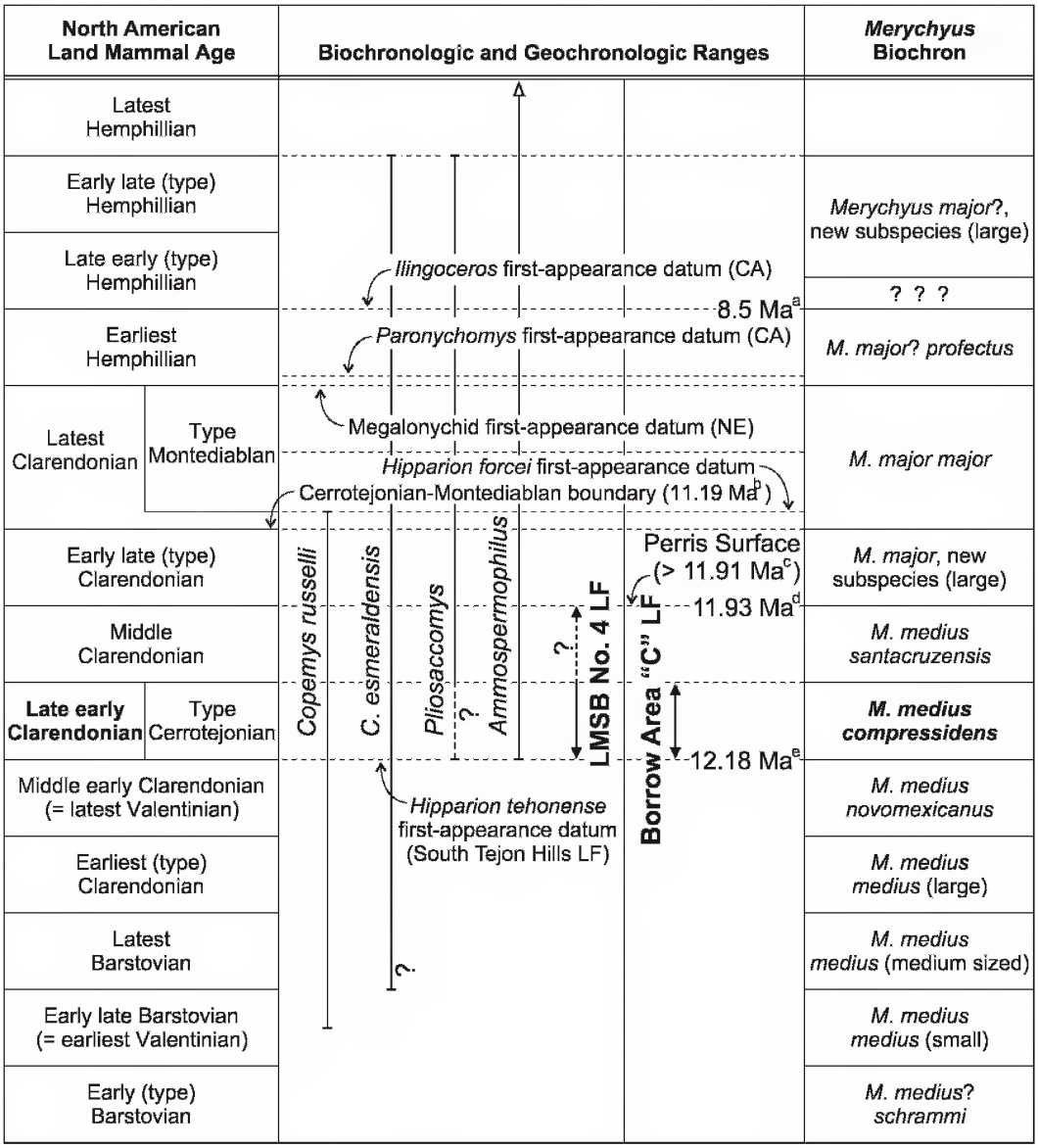

Figure 5 Biochronologic and geochronologic ranges of age-diagnostic rodent taxa and of LMSB No. 4 LF and Borrow Area "C" LF of Cajalco Fauna. Sources of radiometric age determinations: **a**, K-Ar, tuff unit Tra-16, bases of middle parts of *Paronychomys/Borophagus littoralis* AZ and Member 6, DSF, Kern County, California (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, sections B, C, E); **b**, interpolation, CPT XII (= tuff unit Tra-6), base of upper part of *Cupidinimus avawatzensis/Paracosoryx furlongi* AZ, immediately above lower basalt unit and base of middle part of Member 4, DSF (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, sections D and E; Perkins et al., 1998:fig. 3, sample epb92-30; M.E. Perkins, written communication, 2006); **c**, K-Ar (converted), Basalt of Hogbacks, above Perris Surface, Riverside County, California (Kennedy, 1977, sample KA–5; Morton and Morton, 1979); **d**, Ar/Ar, Ibex Hollow Ash (?= Tra-2), between lower and middle parts of *C. avawatzensis/P. furlongi* AZ, middle part of Member 3, DSF (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, sections D and E; Perkins et al., 1998:fig. 3, samples epb94-580 and tc89-21a); **e**, K-Ar, Swallow Ash, near base of Minnechaduza Fauna, 1 m above base of Cap Rock Member, Ash Hollow Formation, Cherry County, Nebraska (Skinner and Johnson, 1984; Swisher, 1992; Tedford et al., 2004).

part of overlying Member 6 (Montediablan *Epicyon aphobus/Hipparion forcei* AZ and lower part of *Paronychomys/Osteoborus diabloensis* AZ). Whistler (1991) also reported the occurrence of *U. californicus* in this part of the DSF. Because Wang et al. (1999) assigned *Epicyon aphobus* (Merriam, 1919) to *Epicyon haydeni* (Leidy, 1859), as suggested earlier by R.H. Tedford (personal communication in Whistler, 1991), and *Osteoborus diabloensis* Richey, 1938, to *B. littoralis*, the *E. aphobus/H. forcei* AZ now is called the *E. haydeni/H. forcei* AZ, whereas the *Paronychomys/O. diabloensis* AZ now is termed the *Paronychomys/B. littoralis* AZ (Fig. 2; Prothero and Tedford, 2000; Lander and Whistler, 2002; Tedford et al., 2004; Lander, 2005b). Correspondingly, *B. littoralis* no longer can be regarded as an index taxon of the Cerrotejonian Stage because its junior synonym (*O. diabloensis*) was considered incorrectly to be an index taxon for the Montediablan Stage by Savage (1955). Similarly, *P. tehonensis*, if valid, and *H. tehonense* also cannot be considered Cerrotejonian index taxa because their stratigraphic ranges overlap those of Montediablan index taxa, including *Hipparion forcei* Richey, 1948, in Member 5 of the DSF and in the *E. aphobus/H. forcei* AZ, as shown by Whistler and Burbank (1992:figs. 4 and 5) and Prothero and Tedford (2000:fig. 5).

The P1–M3 length of LACM 4153 (*U. californicus* topotypic specimen) from Member 5 (*U. californicus* stratotype; Whistler and Burbank, 1992:fig. 4) of the DSF at LACM locality 1553 is virtually the same as that for the specimens from the Orinda Formation (Dibblee, 2005a) at UCMP locality V-5926 in the San Francisco Bay area of Contra Costa County in central California (UCMP 55799, crushed palate with I1-C alveoli and P1–M3) and from the *Alligator mefferdi* Quarry pond deposit in the Merritt Dam Member (F:AM 109517) (Fig. 4, Table 1). Skinner and Johnson (1984) referred the latter specimen to *U. major*, whereas Lander (1998, 2005a) assigned all three specimens to *M. major*. However, the P1–M3 lengths of LACM 4153, F:AM 109517, and UCMP 55799 are greater than in any of the specimens, including those from the Kat Channel in the middle part of the Merritt Dam Member, that previously were referred to *M. major santacruzensis* by Lander (2005a, 2005b) and (exclusive of *M. major santacruzensis* holotypic specimen) now are assigned to *M. major*, subsp. nov. (Fig. 4, Table 1). Although incomplete, the external narial opening of LACM 4153 appears comparable in its degree of retraction to that in *M. major*, subsp. nov. Consequently, Lander (2005a) referred all very large, latest Clarendonian individuals (including *U. californicus* holotypic and topotypic specimens, following Lander, 1977, 1998, 2005a) to *M. major major*. The latest Clarendonian land mammal assemblage (Lafayette Ridge LF, new) from UCMP locality V-5926, like that from Member 4 of the DSF (Whistler and Burbank, 1992:fig. 4), also contains the Cerrotejonian equid index taxon *H. tehonense*, which first appears at LACM locality 1414 in Member 4. The Lafayette Ridge LF, from 3 to 6 m above the lower contact of the Orinda Formation (as mapped by Graymer et al. [1994], but not Dibblee [2005a], who mapped contact lower in local section) is based on the assemblage recorded from the Lafayette Ridge locality by Janis et al. (1998, locality CC30B). On the other hand, *U.* cf. *U. californicus* (= *M. major major*, following Lander, 1977, 1998) is one of the taxa used by Savage (1955) to define the succeeding Montediablan Stage. Therefore, the first-appearance datum of *M. major major* is considered to mark the beginning of the Montediablan Stage (Fig. 5), in accordance with the principle "base defines boundary" (Tedford et al., 2004:177). Correspondingly, the Lafayette Ridge LF and, contrary to Whistler and Burbank (1992), the upper part of the *C. avawatzensis/P. furlongi* AZ are regarded as Montediablan rather than Cerrotejonian in age.

The first appearance of *M. major major* in the DSF probably is UCMP 45955 (partial mandible with i1–m3) from UCMP locality V-5637 (Cowden 2). Another large individual (uncataloged UCR [= UCMP] specimen, anterior portion of dentary with roots of i1–m1) also is from the middle part of Member 4. UCMP locality V-5637 lies above the tuff unit (Tra-6 of Whistler, 1969) that, in turn, is shown very low in the middle part of Member 4 by Whistler and Burbank (1992:fig. 3, sections D and E, fig. 4), immediately above the lower basalt unit that comprises the lower part of the member. The tuff layer has been correlated geochemically with CPT XII, which occurs in the Tuff of Ibex Peak at Trapper Creek in southwestern Idaho and has been determined to be 11.19 ± 0.10 Ma in age by extrapolation (Perkins et al., 1995, 1998:fig. 3, sample epb92-30; Perkins and Nash, 2002; M.E. Perkins, written communication, 2006). Consequently, the Cerrotejonian–Montediablan (Mammalian) Stage boundary is approximately 11.19 Ma in age (Fig. 5). UCMP locality V-5637 probably is the first fossil occurrence shown below the upper basalt unit at the top of Member 4 by Whistler and Burbank (1992:fig. 3, section E) (D.P. Whistler, written communication, 2007). The p1–m3 length (165 mm) of UCMP 45955, the second largest individual of *M. major major* measured for this parameter, is immediately above the observed range of p1–m3 lengths for the sample of *M. major*, subsp. nov., from the Kat Channel that Schultz and Falkenbach (1941) assigned to *U. major* (p1–m3 lengths listed mistakenly with P1–M3 lengths in their table 9).

Although Skinner and Johnson (1984) regarded the *A. mefferdi* Quarry pond deposit of Nebraska as being in the lower part of the Merritt Dam Member, the pond deposit, like the Kat and Xmas channels, is included in the middle part of the Merritt Dam Member in this report because laterally equivalent strata exposed in the *Platybelodon* Quarry, as illustrated by Skinner and Johnson (1984:fig. 38, section 61, quarry 72), lie above a channel deposit that has incised into the lowermost part of the Merritt Dam Member. Unfortunately, the stratigraphic relations of the fossil land mammal assemblages from the *A. mefferdi* Quarry pond deposit and the Kat Channel in the middle part of the Merritt Dam Member have not been determined. However, the radiometric age determination for the Davis (?= *Machaerodus*) Ash (11.55 ± 0.12 Ma) suggests that the Xmas–Kat Channel LF and *M. major*, subsp. nov., both of which possibly occur below the ash, are older than the *A. mefferdi* Quarry LF and *M. major major*, which probably are no older than 11.19 Ma in age on the basis of the interpolated age determination for the equivalent of CPT XII in Member 4 of the DSF, in which the tuff unit immediately underlies the lowest local occurrence of *M. major major* (Fig. 2).

The *M. major* holotypic specimen (USNM 439, right maxillary fragment with P3–M2) represents the largest individual of *Merychyus* known from Nebraska and, like the only other very large individual from Nebraska (F:AM 109517 from *A. mefferdi* Quarry pond deposit), probably is from the middle part of the Merritt Dam Member. Contrary to Schultz and Falkenbach (1941), USNM 439 appears to represent an individual approximately the same size as, not smaller than, that represented by the *U. californicus* holotypic specimen (UCMP 21351, crushed partial skull with P3–4 alveoli, M1, and broken M2–3), the largest known individual from California.

Whistler and Burbank (1992:figs. 4 and 5) regarded the highest local occurrences of *U. californicus* (= *M. major major*) from high in the lower part of Member 6 of the DSF (below tuff unit Tra-16 of Whistler, 1969) as earliest Hemphillian in age because they are from a stratigraphic level above the base of the Hemphillian *Paronychomys/B. littoralis* AZ. The base of the *Paronychomys/B. littoralis* AZ is defined by the first-appearance datum of the Hemphillian and earliest Blancan, sigmodontine murid *Paronychomys* Jacobs, 1977, at LACM locality 3776, which occurs in the first prominent silcrete bed above the tuff unit (Tra-15 of Whistler, 1969) that lies at the base of Member 6 (Whistler, 1969; Whistler and Burbank, 1992:figs. 4 and 5; D.P. Whistler, written communications, 2005, 2007). Tuff unit Tra-15 has been determined to be 8.4 ± 1.8 Ma on the basis of a fission-track radiometric dating analysis of zircon crystals (C.W. Naeser, personal communication, 1985, in Cox and Diggles, 1986; Loomis and Burbank, 1988; Whistler and Burbank, 1992:fig. 3, sections B, C, E, fig. 4; Wang et al., 2005) and 9.36 ± 0.20 Ma by extrapolation (Perkins et al. 1998:fig. 3, sample epb92-75). Tedford et al. (2004) also considered the oldest record of *Paronychomys* to be earliest Hemphillian in age. In contrast, Lander (2005a, 2005b) regarded the lowest local occurrence of *Paronychomys* in Member 6 as latest Clarendonian in age because it is from approximately the same stratigraphic level as the highest definite local occurrence of *M. major major*, but far below the first local appearance of the antilocaprid *Ilingoceros* Merriam, 1909 (Fig. 5; Whistler and Burbank, 1992:figs. 4 and 5; Lander, 2005b). Wang et al. (2005) also assigned the fossil land mammal assemblage from LACM locality 3776 to the late Clarendonian NALMA. *Ilingoceros* is a Hemphillian index taxon according to Wood et al. (1941) and, as shown by Whistler and Burbank (1992:fig. 3, sections B, C, E, fig. 4), first appears in the DSF at the base of the middle part of Member 6 in a paleosol associated with tuff unit Tra-16 at LACM locality 5718 (D.P. Whistler, written communication, 2006). *Paronychomys*, on the other hand, was not considered in the definition of the Hemphillian NALMA by Wood et al. (1941). Moreover, this genus is not recorded from the type Montediablan (= latest Clarendonian) Black Hawk Ranch LF, which contains *U.* cf. *U. californicus* (= *M. major major*, following Lander, 1977, 1998) (Savage, 1955). Accordingly and contrary to Whistler and Burbank (1992:figs. 3 and 8), the first appearance of *Paronychomys* and the base of the *Paronychomys/B. littoralis* AZ are considered post–type Montediablan (Figs. 2 and 5; Lander, 2005b). The Black Hawk Ranch LF occurs in the Orinda Formation (Dibblee, 2005c) at UCMP locality V-3310 (Black Hawk Ranch Quarry) in Contra Costa County, central California, approximately 90 m above the basal contact as mapped by Savage (1955), Graymer et al. (1994), and Prothero and Tedford (2000), but not Dibblee (2005c), who mapped the contact lower in the local section.

The highest local occurrence of *U. californicus* in the DSF documented by Whistler and Burbank (1992, figs. 4 and 5) probably is LACM 146300 (right premaxillary fragment with I1–3 roots) from LACM locality 6131. LACM locality 6131 occurs just below tuff unit Tra-16 at the top of the lower part of Member 6 and immediately above the highest prominent silcrete bed shown by Whistler and Burbank (1992:fig. 3, section C, fig. 4) below the tuff unit (D.P. Whistler, written communication, 2005). However, LACM 146300 has a diastema after the I3 and probably is a camelid.

The last appearance of *M. major major* in the DSF is LACM 140735 (partial mandible with i1–m3) from LACM locality 3534 (Powerline Road).

LACM locality 3534 (= UCMP locality V-6739 and LACM locality 3531; 3531 misprinted as 3431 by Whistler [1969]) occurs in the first discontinuous silcrete bed shown by Whistler and Burbank (1992:fig. 3, section E) lying immediately above tuff unit Tra-15 and below the lowest prominent silcrete bed in Member 6 that contains the *Paronychomys* first-appearance datum (Whistler and Burbank, 1992:fig. 4; D.P. Whistler, written communication, 2007). The p1–m3 length (161 mm) of LACM 140735 is very nearly as great as that for the specimen from Member 4 and is very near the upper end of the observed range of this parameter for the specimens from the Kat Channel that Schultz and Falkenbach (1941) assigned to *U. major* (p1–m3 lengths listed mistakenly with P1–M3 lengths in their table 9).

The holotypic specimen (F:AM 14055, partial left dentary with i2–p3 and m1–3) of *M. major*? *profectus*, a member of the late Clarendonian Snake Creek Fauna, is from the Laucomer Member of the Snake Creek Formation in the northwestern Nebraska Panhandle (Skinner et al., 1977). Two topotypic specimens (F:AM 34346 and 43200) are from the base of the member at the F:AM Olcott (Hill) Quarry on Olcott Hill (Skinner et al., 1977:fig. 5), whereas the stratigraphic levels that yielded the holotypic and remaining topotypic specimens have not been determined. The p1–m3 length (136 mm; Schultz and Falkenbach, 1941:table 1) of AMNH FM 14055 is near the middle of the observed range of this parameter for the combined samples from the lower part of the Ash Hollow Formation that Schultz and Falkenbach (1941:table 9) assigned to *U. profectus* and *U. skinneri*, but below that for the sample from the Kat Channel that they assigned to *U. major* (p1–m3 lengths listed mistakenly with P1–M3 lengths in their table 9). However, AMNH FM 14055 is from a stratigraphic interval above the one (Murphy Member) that yielded a fragmentary and supposedly larger individual of *M. major* (AMNH FM 83545) (Skinner et al., 1977; Tabrum, 1981). Skinner et al. (1977) assigned the latter specimen, which lacks the external narial opening, to *U. major* because it appears to represent an individual comparable in size to the holotypic specimen of *M. major major* and the specimens from the Kat Channel that now are referred to *M. major*, subsp. nov. On the basis of the probable presence of a large or very large form of *M. major*, the fauna from the Murphy Member is regarded as late, rather than early, Clarendonian in age, contrary to Skinner et al. (1977) and Tedford et al. (1987, 2004) (Fig. 2). Tedford et al. (1987, 2004) considered the fauna from the Murphy Member to be a correlative of the Minnechaduza Fauna.

Unfortunately, the external narial opening is not even partially preserved in any example of *M. major*? *profectus*, although it presumably was at least as retracted as in its immediate ancestors (*M. major*, subsp. nov., and *M. major major*), but much more retracted than in middle Clarendonian *M. medius santacruzensis*, which, in turn, preceded *M. major*, subsp. nov. Although clearly assignable to *Merychyus*, the holotypic and topotypic specimens of *M. major*? *profectus* are assigned only questionably to *M. major* as a comparatively and secondarily small-bodied subspecies because they might represent a taxon in which the external narial opening is slightly more retracted than in *M. major major*.

An undescribed, large or very large form of *M. major*? occurs in the early Hemphillian *Aphelops* Draw Fauna and the early late Hemphillian ZX Bar LF of the Johnson Member of the Snake Creek Formation, stratigraphically above the Snake Creek Fauna and *M. major*? *profectus* from the Laucomer Member (Fig. 2; Skinner et al., 1977; Lander, 2005a). These youngest reported oreodontoid records are considered to represent a newly recognized subspecies that is distinguished from *M. major*? *profectus* on the basis of its secondarily larger body size (Lander, 2005a).

The Snake Creek Fauna, like the *Aphelops* Draw Fauna and the ZX Bar LF, also contains a megalonychid sloth (Sinclair, 1915; Hirschfeld and Webb, 1968; Lander, 2004, 2005a, 2005b). Skinner et al. (1977), however, suggested that the corresponding specimen (PUM 12079), which had been collected at PUM locality 1000C on Olcott Hill, was mislabeled and, rather than having been found in the Laucomer Member, might have been recovered from the Johnson Member. Skinner et al. (1977), following Wood et al. (1941), noted that sloths did not appear in North America until the Hemphillian NALMA. On the other hand, there is no compelling reason for concluding that PUM 12079 had been mislabeled in terms of its stratigraphic provenance. Moreover, the stratigraphic columnar sections provided by Skinner et al. (1977:fig. 5) indicate that the Johnson Member does not overlie the Laucomer Member at Olcott Hill. Accordingly, Lander (2004, 2005a, 2005b) reassigned the Snake Creek Fauna, including *M. major*? *profectus*, from the late Clarendonian NALMA to the earliest Hemphillian and (2005a) regarded the *Aphelops* Draw Fauna and its record of *M. major*?, subsp. nov., as late early Hemphillian in age. Unfortunately, it has not been demonstrated that the stratigraphic ranges of *M. major*? *profectus* and sloths overlap in the Laucomer Member. Nevertheless, the Snake Creek Fauna is at least partly earliest Hemphillian age on the basis of the presence of a sloth.

LACM 146098 (broken right P1, left P3, left M1, and right M2) represents a secondarily small

form of *M. major* from the lower part of Member 6 of the DSF at LACM locality 6128 (Trudy Quarry) (Lander, 2004, 2005a, 2005b). LACM locality 6128 is below the silcrete bed containing the lowest local occurrence of *Paronychomys* at LACM locality 3776, but just above the highest local occurrence of *M. major major* at LACM locality 3534 (Whistler, 1969; Whistler and Burbank, 1992:fig. 3, section E, fig. 4; G.T. Takeuchi, written communication, 2007; D.P. Whistler, written communication, 2007). The M1 length of LACM 146098 (17.7 mm) is well below the observed range of this parameter for the *M. major major* sample from Member 5 (O.R. = 20.0–27.4 mm on the basis of LACM 4153, 4279, and 29768 and UCMP 21351), much smaller than that (20.2 mm) for the *M. medius santacruzensis* referred specimen (LACM 143524) from Member 3, but similar to that (17.3 mm) for one of the *M. medius compressidens* referred specimens (LACM 29771) from Member 2. This highest local occurrence of *Merychyus* in the DSF is one of the highest local occurrences of *U. californicus* that was documented by Whistler and Burbank (1992:figs. 4 and 5) and, contrary to Lander (2004, 2005a, 2005b), from below the lowest local occurrence that they determined for the Hemphillian index taxon *Ilingoceros*. Because it represents a much smaller individual than those represented by the *M. major major* specimens from lower in the DSF, Lander (2004, 2005a, 2005b) assigned LACM 146098 to earliest Hemphillian *M. major*? *profectus*. Correspondingly, the uppermost part of the *E. haydeni*/*H. forcei* AZ also is earliest Hemphillian rather than latest Clarendonian in age, contrary to Whistler and Burbank (1992, figs. 5 and 8).

Tedford et al. (2004) considered the earliest record of *Ilingoceros* to be late early Hemphillian in age. The lowest local occurrence of *Ilingoceros* in the DSF is from the paleosol that is associated with tuff unit Tra-16, which has been determined to be 8.5 ± 0.13 Ma old on the basis of a K-Ar radiometric dating analysis (Whistler and Burbank, 1992:fig. 3, section E, fig. 4). This radiometric age determination suggests that *M. major*? *profectus* and, therefore, the earliest Hemphillian NALMA are no younger than 8.5 Ma in age (Figs. 2 and 5). Tedford et al. (2004), on the other hand, considered the Clarendonian–Hemphillian NALMA boundary to be around 9.0 Ma old, presumably at least partly on the basis of the first local appearance of *Paronychomys* below tuff unit Tra-16 and above tuff unit Tra-15, which has been determined to be 9.36 ± 0.20 Ma in age by interpolation (Fig. 2; Perkins et al. 1998:fig. 3, sample epb92-75).

According to Wood et al. (1941), Skinner et al. (1977), Breyer (1981), Tedford et al. (1987, 2004), and Stevens and Stevens (2003), definite records of oreodonts (i.e., *Ustatochoerus*) are not known after the Clarendonian NALMA, equivocal Hemphillian occurrences possibly having been reworked from older strata (Skinner et al., 1977). However, the records of *M. major*? *profectus* in the *Paronychomys*/*B. littoralis* AZ and in the Snake Creek Fauna of Nebraska appear to substantiate the existence of Hemphillian oreodonts.

Although Whistler and Burbank (1992:fig. 4) assigned the *E. haydeni*/*H. forcei* and *Paronychomys*/*B. littoralis* AZs to the Montediablan (Mammalian) Stage, the local stratigraphic range of *Paronychomys* in the DSF is mostly, if not entirely, above the highest occurrences of the taxa whose restricted biostratigraphic ranges were used by Savage (1955) to define the Montediablan Stage. These taxa include the equids *Dinohippus leardi* Drescher, 1941 (?= *P. fairbanksi* according to MacFadden, 1998), which now is also known from the type Cerrotejonian South Tejon Hills LF in Kern County, Southern California (Prothero and Tedford, 2000) and no longer can be considered a Montediablan index taxon, *H. forcei* (Fig. 4), and *U.* cf. *U. californicus* (= *M. major major*, following Lander, 1977, 1998, 2005a). On the other hand, *H. forcei* possibly still occurs with *M. major*? *profectus* in the Kendall–Mallory LF of the Orinda Formation (as mapped by Dibblee, 2005b) at UCMP locality V-6107 in Contra Costa County, central California (Edwards, 1976, 1982; MacFadden, 1998; Lander, 2005b). This locality, 395 m above the base of the Orinda Formation (Edwards, 1982), is stratigraphically far above UCMP locality V-5926, which is only 3–6 m above the base of the formation and yielded the first local occurrence of *M. major major* (Lander, 1998), and UCMP locality V-3310 (Black Hawk Ranch Quarry), which is only about 90 m above the base of the formation and also yielded the last local occurrence of *M. major major* and the first local occurrence of *H. forcei*, members of the type Montediablan Black Hawk Ranch LF (Savage, 1955; Lander, 1998; Prothero and Tedford, 2000). However, the Kendall–Mallory LF, unlike the Black Hawk Ranch LF, also contains *Paronychomys* (Lander, 2005b). Therefore, the record (UCMP 112151, partial palate with P1–M2) of *M. major*? *profectus* in the Kendall–Mallory LF, like that from the uppermost part of the *E. haydeni*/*H. forcei* AZ in the lowermost part of Member 6, is considered earliest Hemphillian and post-Montediablan in age (Lander, 2005b). Edwards (1976, 1982) assigned UCMP 112151 correctly to *U. profectus*. As indicated by its P1–4 length (50 mm), UCMP 112151 represents an individual that is substantially smaller than those represented by the older records of *M. major major* from lower in the Orinda Formation at UCMP locality V-5926 (UCMP 55799, P1–4

length = ~69 mm) and the UCMP Black Hawk Ranch Quarry (UCMP 33741 and 33742, dP1–4 lengths = 59 and 62 mm, respectively). Moreover, of the samples from Nebraska that Schultz and Falkenbach (1941) assigned to *Ustatochoerus*, the P1–4 length of UCMP 112151 is within the observed range of this parameter only for the *M. medius compressidens* sample from the lower part of the Ash Hollow Formation that they (1941:table 9) assigned incorrectly to *U. profectus*.

The P1–M3 length (126 mm; Lander, 2004) of LACM 44887 from the LMF is at least slightly less than in any example of *M. medius santacruzensis*, including the holotypic specimen from the Pojoaque Member of north-central New Mexico and the questionably referred specimen from Member 3 of the DSF, as well as *M. major*, subsp. nov., from the Pojoaque Member and from the Kat Channel in the middle part of the Merritt Dam Member of north-central Nebraska; much less than in the *M. major major* referred specimens from Member 5 of the DSF, the lowermost part of the Orinda Formation, and the *A. mefferdi* Quarry pond deposit in the middle part of the Merritt Dam Member; but greater than in any individual of *M. medius medius* from the Cornell Dam and Crookston Bridge members of the Valentine Formation in north-central Nebraska and from the lower part of the "Clarendon Beds" of the Texas Panhandle, and all but one individual of this subspecies from the Devil's Gulch Member of the Valentine Formation; and very nearly as great as in the larger of the two individuals of *M. medius novomexicanus* from the Burge Member of the Valentine Formation (Fig. 4, Table 1). On the other hand, the P1–M3 length of LACM 44887 is very near the mean P1–M3 length for the *M. medius compressidens* sample from the Cap Rock Member and the lower part of the Merritt Dam Member (Fig. 4, Table 1). Moreover, LACM 44887, on the basis of its M1–3 length (77 mm), appears to represent an individual similar in size to that represented by the *M. medius compressidens* referred specimen (LACM 29771; M1–3 length = 74 mm) from the upper part of Member 2 of the DSF. The LMF specimen also appears to represent an individual similar in size to those represented by the *M. major? profectus* holotypic specimen and the referred specimen (LACM 146098) from the lower (but not lowermost) part of Member 6 of the DSF at LACM locality 6128. It was for these reasons that Lander (2004) regarded LACM 44887 as referable either to *M. medius compressidens* or to *M. major? profectus* and either late early Clarendonian or earliest Hemphillian in age, respectively. In addition, the P1–4 length (50 mm) of LACM 44887 is the same as that for the *M. major? profectus* specimen (UCMP 112151) from the Orinda Formation at UCMP locality V-6107 but less than those (~54 mm) for the two specimens of *M. medius santacruzensis* and *M. major*, subsp. nov., from Member 3 of the DSF.

REEVALUATION OF THE AGE OF THE CAJALCO FAUNA AND THE LAKE MATHEWS FORMATION

Of the taxa represented in the LMSB No. 4 LF, *Hypolagus*, *Ammospermophilus*, *Spermophilus*, and *Perognathus* have relatively long biochronologic ranges, each of which, according to Woodburne (1987) and Korth (1994), spans at least four North American land mammal ages. *Ammospermophilus* first appears in the Cap Rock Member of the Ash Hollow at the UNSM Poison Ivy Quarry in north-central Nebraska (Korth, 1997) and is a member of the late early Clarendonian Minnechaduza Fauna.

However, following Korth (1994), the remaining taxa in the LMSB No. 4 LF have comparatively short biochronologic ranges and, therefore, are the more age-diagnostic taxa in the assemblage (Lander and Whistler, 2002). The first appearance of *C. russelli* is in the late Barstovian Upper Barstow Fauna from the upper part of the FTM in the Barstow Formation of Southern California (Lindsay, 1972), and its last appearance is in the latest? Clarendonian Nettle Spring Fauna from the Caliente Formation of Southern California (James, 1963). The earliest record of *C. esmeraldensis* also is in the Upper Barstow Fauna (Lindsay, 1972), and its latest record is in the early late Hemphillian McKay Reservoir and Little Valley LFs from the Shutler and Chalk Butte formations, respectively, of Oregon (Shotwell, 1956, 1967a, 1970). Korth (1994) mistakenly considered *C. esmeraldensis* to be restricted to the Clarendonian NALMA. The oldest occurrence of *Pliosaccomys* is in the late early? Clarendonian Wolf Creek Fauna from the Ash Hollow Formation (Skinner and Johnson, 1984) of southwestern South Dakota (Green, 1956), whereas its youngest occurrence is in the McKay Reservoir and Little Valley LFs (Shotwell, 1956, 1967b, 1970). The early Barstovian occurrence in the Lower Barstow Fauna that Woodburne et al. (1990) and Woodburne (1991) assigned incorrectly to *Pliosaccomys* is the record that Lindsay (1972) and Tedford et al. (1987, 2004) assigned to *Parapliosaccomys* Shotwell, 1967b. On the basis of the former identification, Lander (2004) erroneously considered the first appearance of *Pliosaccomys* to be early Barstovian in age rather than late early? Clarendonian. Tedford et al. (1987, 2004), on the other hand, wrongly regarded the first occurrence of *Pliosaccomys* as earliest Hemphillian in age.

On the basis of the overlapping biochronologic ranges of *Ammospermophilus* and *Pliosaccomys*,

the LMSB No. 4 LF, contrary to Lander and Whistler (2002) and Lander (2004), probably is no older than late early Clarendonian in age (Fig. 5). On the other hand and again contrary to Lander and Whistler (2002), the local fauna is no younger than early late Hemphillian in age if *C. esmeraldensis* is present, but no younger than latest Clarendonian if *C. russelli* is present instead (Fig. 5). However, the apparent absence of the dominantly Hemphillian *Paronychomys*, which is considered to have first appeared at or just after the beginning of the Hemphillian NALMA (Lander, 2005a) and just after the end of the Montediablan Stage, suggests that the LMSB No. 4 LF is no younger than Clarendonian in age (Fig. 5). Moreover, if the LMSB No. 4 and Borrow Area "C" LFs are approximate correlatives, then the oreodontid in the Borrow Area "C" LF is assignable to *M. medius compressidens* rather than to the earliest Hemphillian *M. major? profectus*, and the latter local fauna, in turn, is a correlative of the Minnechaduza Fauna and late early Clarendonian in age (Fig. 5). Similarly, the possible association of *M. medius compressidens* and *C. russelli* in the Cajalco Fauna suggests that the entire fauna, including the unnamed local fauna, is a correlative of the lower and middle parts of the early late Clarendonian *M. medius/C. russelli* AZ in Member 2 of the DSF.

The Swallow and the Davis ashes lie approximately 1 and 15 m above the bases of the Cap Rock and Merritt Dam members, respectively, in the lower part of the Ash Hollow Formation (Skinner and Johnson, 1984) and have been determined to be 12.18 ± 0.12 and 11.55 ± 0.12 Ma in age on the basis of K-Ar radiometric dating analyses (Swisher, 1992; Tedford et al., 2004). These volcanic ash beds roughly bracket the Minnechaduza Fauna and the local stratigraphic range of *M. medius compressidens* in the lower part of the Ash Hollow Formation.

Tuff unit Tra-1 lies about 113 m above the base of the DSF in Member 2 and is the unit that has been correlated geochemically with CPT V, which has been determined to be 12.071 ± 0.037 and 12.169 ± 0.032 Ma in age on the basis of Ar/Ar radiometric dating analyses (Perkins et al., 1998:fig. 3, table 7, samples epb92-40, wjr93-436, and tc89-18a; Perkins and Nash, 2002; Tedford et al., 2004; M.E. Perkins, written communication, 2006). Tuff unit Tra-1 is bracketed by LACM localities 6620 and 1108 (D.P. Whistler, written communication, 2005), both of which have yielded *M. medius*, and separates the lower and middle parts of the *M. medius/C. russelli* AZ.

Tuff unit Tra-3 in Member 3 of the DSF has been determined to be 11.8 ± 0.9 Ma in age on the basis of a zircon fission-track radiometric dating analysis (Whistler and Burbank, 1992:fig. 3, section F; Perkins et al., 1998:fig. 3, sample epb92-42). Another tuff bed from slightly lower in the DSF has been correlated with the Ibex Hollow Ash, which has been determined to be 11.93 ± 0.030 Ma in age (standardized relative to radiometric age determination for Fish Canyon Tuff by Perkins et al., 1998:fig. 3, table 7) on the basis of an Ar/Ar radiometric dating analysis (Perkins et al., 1995, 1998:fig. 3, samples epb94-580 and tc89-21a; Perkins and Nash, 2002). The equivalent of the Ibex Hollow Ash in the DSF probably is tuff unit Tra-2, which is shown above the top of the *M. medius/C. russelli* AZ and the highest stratigraphic occurrences of *C. russelli* and *M. medius compressidens* by Whistler and Burbank (1992:fig. 4).

The radiometric age determinations for the three tuff units in the DSF are bracketed by those for the Swallow and Davis ashes and corroborate the faunal correlation of the *M. medius/C. russelli* AZ and the Minnechaduza Fauna presented in this report (Fig. 2). The radiometric age determinations for the Davis and Ibex Hollow ashes suggest that the Minnechaduza and Cajalco faunas and at least the middle and upper parts of the *M. medius/C. russelli* AZ are between 12.18 and 11.93 Ma old (Figs. 2 and 5) and, following Lourens et al. (2004), late middle Miocene in age. Moreover, the radiometric age determination for the Swallow Ash implies that the older records of the Minnechaduza Fauna are about the same age as the lower part of the Cerrotejonian *M. medius/C. russelli* AZ, assuming the younger radiometric age determination for CPT V is the more reliable of the two (Fig. 2). Correspondingly, these radiometric age determinations also suggest that the Burge Fauna, which occurs below the Swallow Ash and the Minnechaduza Fauna, probably is too old to be a correlative of the *M. medius/C. russelli* AZ or the lower part of the stratigraphically overlying *C. avawatzensis/P. furlongi* AZ, contrary to Tedford et al. (2004) and Whistler and Burbank (1992:fig. 5), respectively. On the other hand, if the older radiometric age determination for CPT V is the more reliable of the two, then the lower part of the *M. medius/C. russelli* AZ probably is older than the Minnechaduza Fauna and might be a correlative of the Burge Fauna, following Tedford et al. (2004) (Fig. 2). Consequently, the oreodont remains from LACM locality 6620 might be assignable to *M. medius novomexicanus* rather than *M. medius compressidens*.

An age greater than 11.93 Ma for the Cajalco Fauna and the LMF is consistent with an age as old as 11.91 ± 0.13 Ma for the Basalt of Hogbacks (Kennedy, 1977, sample KA–5; converted by Morton and Morton, 1979), which overlies the Perris Surface southeast of Lake Mathews (Fig. 5). The Perris Surface, in turn, overlies the LMF and the Cajalco Fauna (Fig. 5; Woodford et al., 1971). Moreover, contrary to

Lander (2004, 2005a), the Cajalco Fauna is at least 2.55 Ma too old to be earliest Hemphillian in age on the basis of radiometric age determinations for the Basalt of Hogbacks and tuff unit Tra-15 at the base of Member 6 of the DSF (Fig. 5). Tuff unit Tra-15 has been determined to be only 9.36 ± 0.20 Ma in age by extrapolation (Fig. 2; Perkins et al. 1998:fig. 3, sample epb92-75).

CONCLUSIONS

1. The upper part of the Miocene continental Lake Matthews Formation in the northern Peninsular Ranges Province of Southern California is truncated by the Perris Surface. A probable outlier of this surface is overlain by the Basalt of Hogbacks, which has been determined to be as old as 11.91 ± 0.10 million years in age.
2. The Cajalco Fauna of the Lake Matthews Formation consists of three local faunas: the Lake Mathews Sediment Basin No. 4 LF and the Borrow Area "C" LF, both of which are new names, and an unnamed local fauna.
3. The LMSB No. 4 LF includes a leporid (*Hypolagus*), a sciurid (*Spermophilus* or *Ammospermophilus*), a heteromyid (possibly *Perognathus*), a geomyid (*Pliosaccomys*), and a cricetodontine murid (*C. esmeraldensis* and/or *C. russelli*).
4. The Borrow Area "C" LF includes a medium-sized tapirlike ticholeptine oreodontid (*M. medius compressidens*) and medium-sized and large camelids.
5. The unnamed local fauna includes a camelid, and a felid is either a member of this unnamed local fauna or of the Borrow Area "C" LF.
6. On the basis of the overlapping biochronologic ranges of *Ammospermophilus*, *Pliosaccomys*, *Copemys*, and *M. medius compressidens*, and the radiometric age determinations for the Basalt of Hogbacks, tuff units Tra-1 and Tra-2 of the DSF in the western Mojave Desert of Southern California, and the Swallow and Davis ashes in the Ash Hollow Formation of north-central Nebraska, the Cajalco Fauna is late early Clarendonian in age and a correlative of the *M. medius/C. russelli* AZ in Member 2 of the DSF of California and the Minnechaduza Fauna in the Cap Rock Member and the lower part of the overlying Merritt Dam Member in the Ash Hollow Formation of Nebraska.
7. The Devil's Gulch Fauna from the Devil's Gulch Member of the Valentine Formation, which underlies the Ash Hollow Formation in Nebraska, contains a comparatively large form of *M. medius medius* that also occurs in the type Clarendonian Lower Clarendon Fauna from the lower part of the "Clarendon Beds" (= Ogallala Formation) in the Texas Panhandle. Consequently, the Devil's Gulch Fauna is earliest Clarendonian rather than latest Barstovian in age.
8. *Merychyus major*? *profectus*, a secondarily small form of *M. major*, and a megalonychid sloth occur in the Snake Creek Fauna from the Laucomer Member of the Snake Creek Formation in the northwestern Nebraska Panhandle. Therefore, the Snake Creek Fauna and *M. major*? *profectus* are earliest Hemphillian rather than late Clarendonian in age.
9. The first appearance of *M. major*? *profectus* in the DSF is in the uppermost part of the *E. haydeni/H. forcei* AZ in the lowermost part of Member 6, immediately above the last local appearance of *M. major major* and below the first local appearance of *Paronychomys*. Correspondingly, the uppermost part of the *E. haydeni/H. forcei* AZ also is earliest Hemphillian rather than latest Clarendonian in age.

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Excavation monitoring that allowed for the recovery of any large fossil remains that might have been uncovered by excavation of LMSB No. 4, the collection and initial processing of the fossil-bearing sedimentary rock sample from the LMF to allow for the recovery of small fossil land mammal remains that were too small to be observed by a monitor, and the recording of associated geologic and geographic fossil locality data were conducted by Messrs. David A. Alexander, Jeffrey D. Cassidy, and Michael H. Stevens, PEAI paleontologic construction monitors. Their work was supervised by Mr. Mark A. Roeder, a PEAI field and laboratory supervisor. Final processing of the rock sample and identification and analysis of the fossil remains that were recovered as a result of sample processing were conducted by Dr. David P. Whistler, formerly a PEAI senior vertebrate paleontologist and curator emeritus of vertebrate paleontology at the LACM. Dr. Whistler also assisted in preparing the mitigation program final technical report of results and findings (Lander and Whistler, 2002) that is the basis for this contribution and generously provided stratigraphic data on the oreodont and other LACM specimens from the DSF.

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file at the AMNH and in which he had extensively annotated the entry for each of these specimens with its original stratigraphic data. In some cases, he had updated the data in his copy with the more recent stratigraphic nomenclature that had been presented by Skinner et al. (1968) or that would be published subsequently by Skinner and Johnson (1984). Drs. Jin Meng (curator in charge) and Christopher A. Norris (director of collections and archives), Denny V. Diveley (former F:AM collections administrator), Ivy S. Rutzky (senior scientific assistant of fossil fish), Susan K. Bell (senior scientific assistant), and Michele Spaulding granted access to the AMNH and F:AM Merychyus fossil collections and archives; provided measurements, locality data, and AMNH catalog numbers for a number of uncataloged F:AM specimens; or offered assistance during my 2003 visit to the AMNH.

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This study was initiated as part of a larger systematic review of the Oreodontidae (Lander, 1977, 1998), a study originally suggested as a possible thesis topic in 1968 by the late Dr. James Reid Macdonald, then of the LACM. After having reviewed his copy of Schultz and Falkenbach (1968), he stated that the family appeared to have been oversplit taxonomically by the latter authors and, therefore, still was in need of extensive revision.

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Heteromyid rodents from Miocene faunas of the Mojave Desert, Southern California

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ABSTRACT. Four species of small heteromyid rodents from Miocene deposits in or near the Mojave Desert of Southern California are similar in size and crown height; these features have made their identification and characterization difficult. These species are *Paratrogomys whistleri* gen. et sp. nov.; *Korthomys formicarum* (Wood, 1935) gen. nov., with a new generic assignment; *Mioheteromys crowderensis* sp. nov.; and *Proheteromys sulculus* Wilson, 1960. *Paratrogomys whistleri* is known only from the Crowder Formation in the Mojave Desert; *K. formicarum* is known from the lower Harrison Formation in Nebraska, the Anceney Fauna in Montana, and the Barstow Fauna in the Mojave Desert; *M. crowderensis* is known from both the Crowder Formation and the Barstow Formation in the Mojave Desert; and *P. sulculus* is known from the Quarry A Fauna in Colorado and the Crowder Formation in the Mojave Desert. *Proheteromys sulculus* is considered herein distinct relative to the species described as *Proheteromys sulculus* from the Vedder Fauna in Southern California by Lindsay (1974).

The specimens described herein are lower crowned than the material described as *Perognathoides* by Wood (1936), now considered as *Cupidinimus* Wood, 1935, the common heteromyid rodent recorded from the Barstow Formation and, collectively, they probably represent a poorly defined "stage" in the middle Miocene evolution of the Heteromyidae. The sample size of these species is now considered sufficiently large to provide minimal characterization of these rodents. *Paratrogomys whistleri* has mesodont cheek teeth, a sulcate upper incisor, and p4 with weak union of the narrow protolophid that is oriented subparallel relative to the metalophid. *Korthomys formicarum* is similar in size to these other small rodents, but it is brachydont, with inflated bunodont cusps. The P4 of *K. formicarum* (previously unknown) is relatively large, suggesting possible affinity with Florentiamyidae. *Mioheteromys crowderensis* has mesodont cheek teeth with a sulcate upper incisor, as in *P. whistleri*; it differs from *P. whistleri* by having p4 with a narrow protolophid oriented obliquely relative to the metalophid. *Proheteromys sulculus* was thoroughly described by Wilson (1960) from the Quarry A Fauna in Colorado; it has mesodont cheek teeth and a sulcate upper incisor with a more shallow surface separation or "step" compared with the upper incisor of *P. whistleri* and *M. crowderensis*; p4 of *P. sulculus* usually has the protolophid oriented obliquely relative to the metalophid, as in *M. crowderensis.* In these species of heteromyid rodent, the metaloph of upper molars and the metalophid of lower molars are usually J-shaped after moderate wear. These J-shaped lophs and lophids, along with the mesodont height of crown (except for *K. formicarum*) are considered their most distinctive features.

INTRODUCTION

Heteromyid rodents (considered a subfamily of the family Geomyidae Bonaparte, 1845, by McKenna and Bell [1997:183]; but considered a family by Flynn et al. [in press]) are a very successful group of small North American mammals, with a fossil record that began in the late Oligocene (e.g., Arikareean North American Land Mammal Age [NALMA]). They were probably derived from earlier heliscomyid rodents in North America and inhabited North America during most of the Neogene. During the late Neogene, heteromyid rodents dispersed from North America into Central America and northern South America.

Study of fossil heteromyid rodents was undertaken by A.E. Wood for his doctoral dissertation in 1931, and during much of the 20th Century, his review of the Heteromyidae (Wood, 1935) has been a guiding reference for study of systematic relationships of heteromyid rodents and their relatives. Another early review of heteromyid rodents was undertaken by W.G. Reeder for his

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doctoral dissertation in 1956. Unfortunately, much of Reeder's dissertation has never been published.

From 1935 through the 1970s, most of the studies of small fossil rodents were based primarily on teeth, the most commonly preserved remains of these small mammals. During the 1980s J.H. Wahlert published several papers (Wahlert, 1983, 1984, 1985) on the cranial foramina and skull morphology of fossil rodents, which provided additional characters for interpreting their history and stimulated new studies of phylogenetic relationships among rodents. Wahlert (1985) described important skull morphology of geomyoid rodents, redefining this group and their nearest relatives (Geomorpha) on the basis of both cranial and mandibular morphology. Later, Wahlert (1991) recognized a new subfamily (Harrymyinae) of Miocene heteromyids, demonstrating the utility of cranial morphology as a phylogenetic tool, as well as illustrating previously unrecognized taxonomic diversity among fossil heteromyid rodents. More recently, Korth (1997) established another subfamily of Miocene fossil heteromyids, the Mioheteromyinae, on the basis of both cranial and dental characteristics. Korth elaborated further on heteromyid relationships, placing the Harrymyinae and Mioheteromyinae phylogenetically among the primitive early radiation of the Heteromyidae. We anticipate that additional diversity of Miocene heteromyids will be recognized with further study. This report is an attempt to add more dental and cranial features to the Miocene heteromyid database with the goal of clarifying dental characters of these rodents, and thereby enhancing our interpretations of this complex rodent group.

Cranial material is preserved for some of the species we describe in this paper, but much of the cranial material is inadequately prepared and, therefore, not fully utilized in this study. We invite interested researchers to prepare and study the skull material of these rodents and to add to the characterization of these fossils, which might refute or support some of the conclusions we present.

Stratigraphic relationships of the fossil sites in the Crowder Formation can be found in the paper presented by Reynolds et al. (2008). These fossils and sites were first reported by Reynolds (1991). Stratigraphic relationships of the fossil sites in the Barstow Formation can be found in Lindsay (1972, 1995).

In keeping with our unsettled but maturing views of heteromyid systematics and our inadequate knowledge of cranial characteristics
of these rodents, we place these genera in a familial framework of Heteromyidae *incertae sedis*.

METHODS AND MATERIALS

Fossils were obtained primarily by screen washing sediments from selected locations. Measurements of specimens were made with an optical micrometer and rounded to the nearest 0.1 mm. All measurements are maximum dimensions, with anteroposterior length perpendicular to transverse width, positioning the side of the tooth vertical (or as vertical as possible) unless otherwise indicated. All specimens are curated in the San Bernardino County Museum (SBCM).

Dental terminology (Fig. 1) generally follows that of Korth (1994:fig. 15.2) with the following exception: Korth's p4 metaconid is considered the protoconid. Designation of protoloph, metaloph, protolophid, metalophid, and hypolophid follow that of Lindsay (1972:fig. 19, 1974:fig. 1), but in contrast to the terminology of Lindsay (1972, 1974), the large cusp on the lingual side of the P4 metaloph is called the entostyle rather than the hypostyle. A smaller cusp posterior to the entostyle on the posterior cingulum of P4 is called the hypostyle (see Fig. 1). The three principal cusps on the metaloph of the P4 are therefore called the metacone, hypocone, and entostyle in this study. Upper cheek teeth are designated with upper case (e.g., M1) and lower cheek teeth with lower case (e.g., m1) following the convention adopted by editors of the *Journal of Vertebrate Paleontology*.

ABBREVIATIONS

CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania USA
KU	Natural History Museum, University of Kansas, Lawrence, Kansas USA
NALMA	North American Land Mammal Age
SBCM	San Bernardino County Museum, Redlands, California USA
UALP	Laboratory of Paleontology, University of Arizona, Tucson, Arizona USA
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
UCR	Department of Geological Sciences, University of California, Riverside, California, collections and records now maintained at the Museum of Paleontology, University of California, Berkeley, California USA

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Rodentia Bowdich, 1821

Geomyoidea Bonaparte, 1845

Heteromyidae Gray, 1868

Heteromyidae *incertae sedis*

***Paratrogomys* new genus**

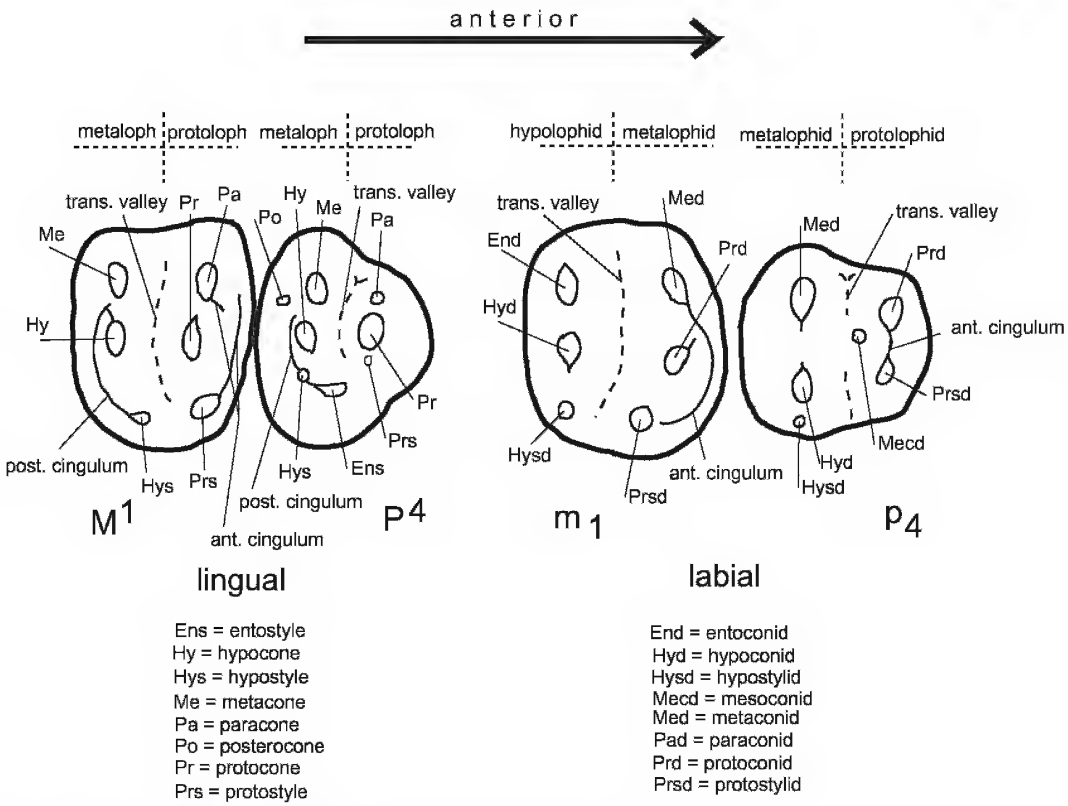

Figure 1 Dental terminology used in describing heteromyid teeth.

TYPE AND ONLY INCLUDED SPECIES. *Paratrogomys whistleri* sp. nov.

DISTRIBUTION AND AGE. Lower Crowder Formation, Cajon Valley, Southern California; Wye Local Fauna (Reynolds et al., 2008); late Hemingfordian NALMA.

DIAGNOSIS. The same as for species, until further species are described.

ETYMOLOGY. The generic name refers to the similarity to *Trogomys* Reeder, 1960; *para-* (Greek) meaning beside, near, or beyond.

DISCUSSION. *Paratrogomys* is similar to *Trogomys rupinimenthae* Reeder, 1960, a small heteromyid rodent from Hemingfordian deposits of the Tick Canyon Formation in the eastern Ventura Basin of Southern California. A second record of *Trogomys* (*Trogomys* cf. *T. rupinimenthae*) was described by Whistler (1984) from Hemingfordian sediments of the Arkose Member of the Kramer Beds near Boron in the Mojave Desert of Southern California. This is the third report of a *Trogomys*-like rodent from Hemingfordian deposits in Southern California. On the basis primarily of cranial characters, *Trogomys* was placed in the heteromyid subfamily Mioheteromyinae by Korth (1997). *Cupidinimus* Wood, 1935, is also a common middle Miocene heteromyid rodent genus with mesodont cheek teeth; however, *Cupidinimus* is higher crowned than *Paratrogomys*, with more vertical sides of teeth, better developed lophs, generally fewer accessory cusps, and bases of the roots commonly fused, in addition to the primary difference, having greater height of crown.

Dentally, Korth (1997) characterized the Mioheteromyinae (in part) on noncentral union of p4 lophids, with union of the lophids labial to the midline but not at the labial end of the metalophid; that is, having a "central enamel pit" rather than an X-pattern on the p4, a character of the Perognathinae (and Dipodomyinae) recognized by Wood (1935:211–212). Thus, the Mioheteromyinae were conceived as a primitive stage of evolution among the Heteromyidae, in contrast to the derived stage of evolution represented by the Perognathinae, Heteromyinae, and Dipodomyinae. Recognition and characterization of the Mioheteromyinae as a primitive Miocene diversification of heteromyids is one of the significant advances in our understanding of the evolution of Heteromyidae, for which Korth (1997) is applauded.

However, it appears that the relationship proposed by Korth is more complex than he realized. Thus, we are reluctant to assign *Paratrogomys*

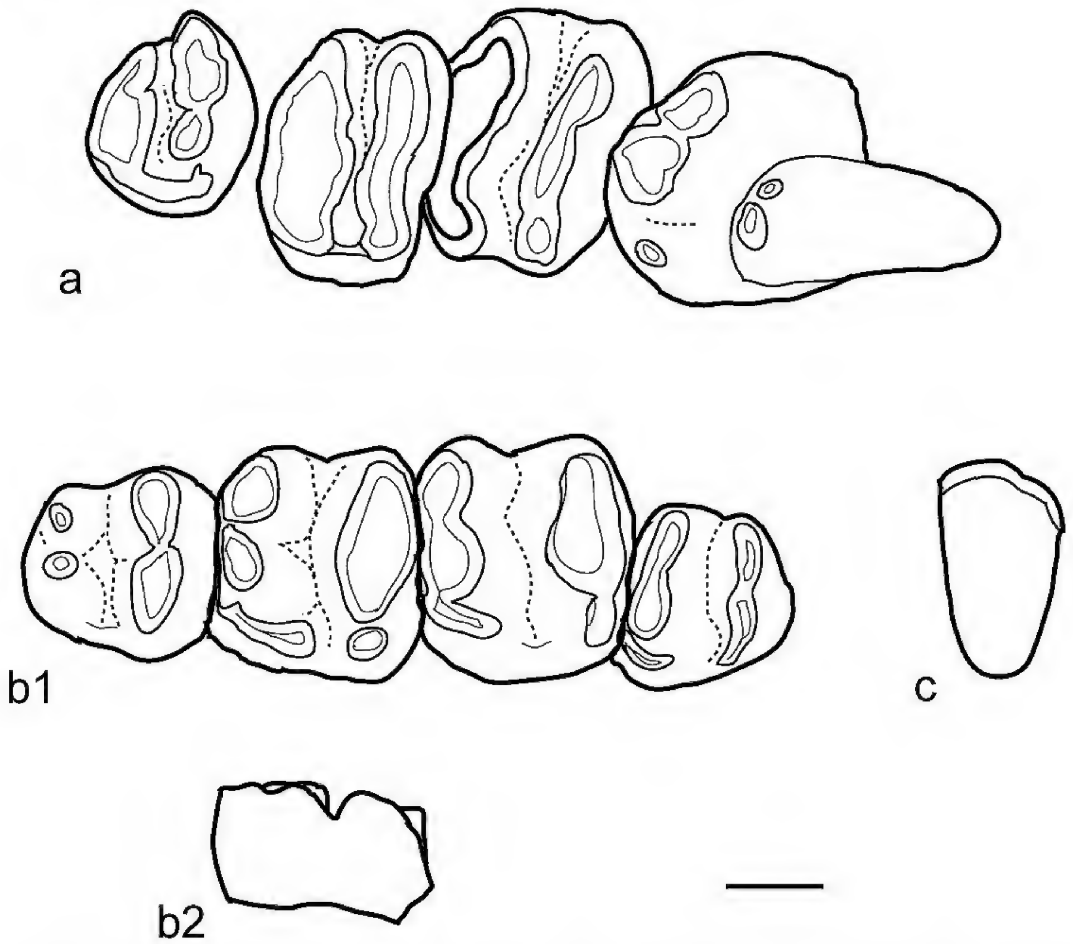

Figure 2 Line drawings of *Paratrogomys whistleri* gen. et sp. nov. HOLOTYPICAL SPECIMEN L1585-1412: **a,** occlusal view of partial skull with right P4–M3; **b1,** occlusal view of left p4–m3; **b2,** labial view of left m1; L1585-1492: **c,** cross section of upper incisor. Scale bar = 1 mm.

(plus *Korthomys* and *Mioheteromys*) to the subfamily Mioheteromyinae until features of the other heteromyid subfamilies (e.g., Perognathinae, Dipodomyinae, Heteromyinae, and Harrymyinae) are better characterized relative to the Miocene record of Heteromyidae; we assign *Paratrogomys* to Heteromyidae *incertae sedis*.

Paratrogomys whistleri new species
Figures 2 and 3

HOLOTYPE. SBCM L1585-1412, anterior part of cranium with upper incisors, right maxilla with P4 and M1–3, left maxilla with P4 and M1–2, right dentary with p4 and m2–3, left dentary with p4 and m1–3.

HYPODIGM. Holotype plus 67 referred specimens, all SBCM, as follows: L1585-317 left m2; L1585-393, right m3; L1585-394, left m3; L1585-496, right maxilla with dP4–M1; L1585-1413, block of sediment with broken bone that yielded isolated RI1, Rp4, and Rm1; L1585-1415, isolated right dP4, left maxilla with dP4–M1, isolated right P4, isolated right M3, and isolated left M2; L1585-1416, edentulous right maxilla; L1585-1417, palate with right P4–M1 and left P4–M1; L1585-1418, right dP4–M1; L1585-1419, left P4; L1585-1420, left P4; L1585-1421, right P4; L1585-1422, right P4; L1585-1423, left P4; L1585-1424, left P4; L1585-1426, left P4; L1585-1428, right P4; L1585-1429, right P4; L1585-1431, left dentary with m1–m3; L1585-1432, right m1; L1585-1433, left m2; L1585-1434, left M1; L1585-1435, left M2; L1585-1436, right M1; L1585-1437, left M2; L1585-1438, right M1; L1585-1439, left M2; L1585-1440, left M2; L1585-1441, left M2; L1585-1442, left P4; L1585-1443, right M1; L1585-1444, right M1; L1585-1445, right M1; L1585-1446, left M2; L1585-1447, right m1; L1585-1448, left M1; L1585-1449, left M2;

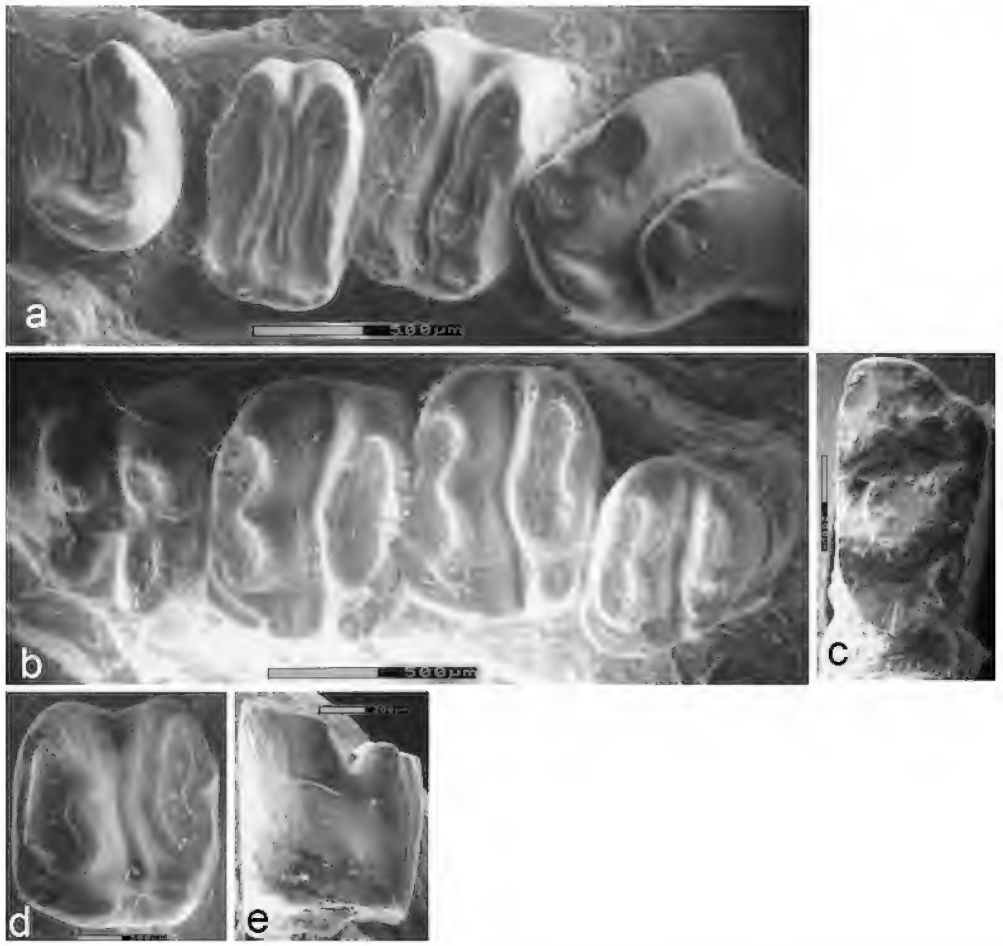

Figure 3 SEM photos of *Paratrogomys whistleri* gen. et sp. nov. HOLOTYPICAL SPECIMEN L1585-1412: **a,** occlusal view of right P4–M3 (as in Fig. 2a); **b,** occlusal view of left p4–m3 (as in Fig. 2b1); **c,** L1585-1492 cross section of upper incisor (as in Fig. 2c); **d,** occlusal view; **e,** labial view of left m1 (as in Fig. 2b1 and 2b2). Scale bars: a, b = 500 μm; c, d, e = 200 μm.

L1585-1450, left M3; L1585-1451, right M2; L1585-1452, right M3; L1585-1453, right M2; L1585-1454, left M3; L1585-1455, left dentary with i1 and p4; L1585-1456, left p4; L1585-1458, left P4; L1585-1461, right p4; L1585-1462, right p4; L1585-1464, left p4; L1585-1465, left m1; L1585-1466, left m1; L1585-1467, left m1; L1585-1468, right m1; L1585-1469, right m1; L1585-1470, left m2; L1585-1471, left m1; L1585-1473, left m2; L1585-1474, left m2; L1585-1475, left m2; L1585-1476, right m2; L1585-1477, right m2; L1585-1478, right m2; L1585-1480, right m3; L1585-1481, right M2–3 and isolated m3; L1585-1482, right P4; L1585-1483, right M1 and left m2; L1585-1492, upper incisor; L1585-1508, left p4.

DISTRIBUTION AND AGE. Lower part of the Crowder Formation, Mojave Desert, Southern California, late Hemingfordian NALMA.

DIAGNOSIS. Small rodent with mesodont cheek teeth and sulcate upper incisors; upper incisors relatively narrow, with shallow "step" separating levels on anterior face, enamel thin.

p4. Lacking (or weak development of) central enamel pit, with narrow protolophid oriented subparallel relative to metalophid; protolophid and metalophid unite initially after moderate wear through minute mesoconid or low medial lophid near (or slightly labial to) midline; minute hypostylid usually present on labial metalophid.

Lower molars. Bilophate with metalophid and hypolophid of subequal width or metalophid slightly wider than hypolophid; lophids unite both labially and centrally in late wear; metalophid becomes J-shaped with wear, and the hypolophid remains straight; hypostylid present on m1 and m2, absent on m3.

P4. With both lingual and medial union of protoloph and metaloph in late wear, protocone elongated transversely and occasionally with minute labial accessory cuspule (?paracone), metacone placed slightly anterior relative to hypocone, hypostyle absent on metaloph.

Upper molars. Bilophate with protoloph and metaloph subequal in width or protoloph slightly wider than metaloph; lophs unite lingually after moderate wear; protoloph is very straight; metaloph is J-shaped (slightly flexed at posterolingual corner of tooth); anterior cingulum discontinuous; transverse valley broader labially resulting from labial thinning of lophs, posterocone absent; in M3, protostyle and hypostyle are indistinct, incorporated into a continuous posterior cingulum.

Paratrogomys gen. nov. differs from *Trogomys* Reeder, 1960, in having the following features: sulcate upper incisors; protolophid of p4 not oriented obliquely relative to metalophid; better (earlier) union of protolophid and metalophid on p4; m3 hypolophid narrow, lacking hypostylid; P4 protoloph more expanded transversely, and in some individuals bears minute accessory cuspule.

Paratrogomys shares with *Trogomys* narrow protolophid on p4 that sometimes retains remnant of anterior cingulum; having minute hypostylid on p4; usually with labial initial union of lophids in lower molars; large entostyle on P4; union of lophs in upper molars usually lingual to midline.

Paratrogomys differs from *Mioheteromys* Korth, 1997, by having p4 with subparallel orientation of protolophid and metalophid; p4 has minute hypostylid; initial union of lophids in lower molars never central; m3 hypolophid narrower and lacks hypostylid; P4 union of protoloph not as well developed lingually; anterior cingulum of upper molars less well developed. *Paratrogomys* differs from *Proheteromys* Wood, 1932, by having p4 with subparallel orientation of protolophid and metalophid; lower molars with less prominent anterior cingulum; P4 lingual union of protoloph and metaloph less well developed; upper molars with later (in wear) lingual union of lophs; M3 with cusps better developed. *Paratrogomys* differs from *Korthomys* gen. nov. by having greater crown height with cusps less inflated.

ETYMOLOGY. Named in honor of David P. Whistler, in recognition of his numerous contributions to vertebrate paleontology and biostratigraphy in Southern California, especially in the Mojave Desert.

DESCRIPTION. Small rodent with large perforation on the rostrum; incisive foramina apparently narrow and short; premaxillary–maxillary suture indistinguishable; auditory bullae unknown; masseteric ridge extends anterior and ventral relative to p4; mental foramen well anterior and lower than anterior end of the masseteric ridge; upper incisors sulcate, relatively long and narrow, with a shallow "step" separating levels on the anterior surface; lower incisors narrow, slightly rounded anteriorly.

p4. Lacking a central enamel pit, with protolophid and metalophid united subcentrally after moderate wear; protolophid narrower than and oriented subparallel relative to the metalophid; a minute "mesoconid" or, alternatively, a long, low, and straight medial loph join the lophids after moderate wear; labial cusps (e.g., protostylid and hypostylid) unite labial to the midline after moderate wear, and lingual cusps (e.g., protoconid and metaconid) join after more wear; metaconid slightly larger than hypoconid, with cusps uniting after early wear; metalophid cusps larger than cusps of protolophid (protoconid and protostylid), with protostylid slightly larger and higher than protoconid; in three of nine specimens, the protoconid has a minute anterolabial ridge (called the anterior cingulum by Reeder [1960]) directed ventrally and labially, joining the protostylid anteriorly or medially after moderate wear; minute hypostylid on labial end of metalophid.

m1. Metalophid and hypolophid subparallel and subequal in width; lophids joined in late wear, initially on labial side and later near center of tooth; in unworn teeth, metalophid slightly higher than hypolophid; four prominent cusps, with medial cusps (protoconid and hypoconid) slightly larger and wider than lingual cusps (metaconid and entoconid); entoconid and hypoconid united after early wear; metaconid and protoconid united with more wear; smaller labial cusps (protostylid and hypostylid) are separate until late wear, with the protostylid slightly higher than the hypostylid; metalophid J-shaped, with protostylid placed slightly posterior relative to protoconid; hypolophid straight, with hypostylid placed lingual to hypoconid and usually isolated until late wear; anterior cingulum prominent, flexed to join the anterior side of the metaconid with the protostylid; posterior cingulum weakly developed or indistinct; posterocuspid absent.

m2. Slightly smaller than m1; metalophid slightly wider and higher than the hypolophid; lophids united after moderate wear, usually labially before medially; both protostylid and hypostylid smaller than on m1; anterior cingulum joins anterolabial side of metaconid; other cusps and lophids as seen in m1.

m3. Smaller size than m2, with hypolophid much narrower than metalophid; lophids joined only after very late wear; hypostylid absent or indistinct; anterior cingulum joins metaconid only after late wear; other cusps and lophids as seen in m2.

dP4. Protoloph with a small, isolated anterocone on the midline anterior to and lower than the small paracone and larger protocone; proto-

loph lower and narrower than the metaloph, joining the metaloph by a prominent noncuspate lingual cingulum; metaloph bicuspid with the metacone smaller and placed slightly anterior relative to the hypocone; lingual cingulum joins the lingual side of the protocone and posterior side of the hypocone, continuing labial to the hypocone as a minute loph (or posterocone) posterior to and between the metacone and hypocone.

P4. Double union (central and lingual) of protoloph and metaloph in late wear; protoloph lower than the metaloph with protocone much wider (transversely) than long (anteroposteriorly), in some individuals (five of 15 specimens) with a minute labial accessory cusp; entostyle large, located anterior relative to the hypocone and metacone, oriented almost perpendicular to the metaloph; no hypostyle on metaloph; metacone placed slightly anterior relative to the hypocone; posterior cingulum present but variable, always joining hypocone and entostyle, sometimes continuing to join the metacone.

M1. Bilophate, wider than long, with unworn protoloph slightly lower than metaloph; protoloph subequal in width or slightly wider than metaloph; lophs joined lingually after moderate wear; protoloph is very straight, with protostyle placed lingual or slightly anterior relative to protocone; metaloph is slightly curved lingually (J-shaped) with hypostyle placed anterior relative to the hypocone, resulting in a rounded posterolingual corner of the tooth; four prominent cusps, with prominent cusps of the protoloph (paracone and protocone) and metaloph (metacone and hypocone) elongated transversely and joined after early wear; protostyle and hypostyle small size, with the hypostyle slightly higher and larger than the protostyle; the hypostyle partially blocks the transverse valley; anterior cingulum discontinuous, usually represented by a short vestige of loph ("pseudoparaconule") directed lingually from the anterior side of the paracone, rarely represented by a short loph directed labially from the anterior side of the protostyle; posterior cingulum low and narrow, usually joining posterior hypocone and hypostyle, occasionally joining posterior metacone and hypocone; transverse valley relatively straight, expanding near labial margin resulting from "thinning" of lophs labially; posterocone absent.

M2. Slightly smaller than M1, with protoloph equal in width or slightly wider than metaloph; height of unworn protoloph and metaloph subequal; anterior cingulum less well developed ("pseudoparaconule" rarely distinct) than on M1; other characters as seen in M1.

M3. Much smaller and narrower than M2, with protoloph and metaloph firmly united lingually (usually united labially, as well); metaloph very curved; metacone minute or indistinct; protostyle small but distinct, hypostyle elongated and joining protostyle; posterior cingulum continuous, joining hypostyle, hypocone, and metacone; other characters as seen in M2.

Measurements of *Paratrogomys whistleri* are given in Table 1.

DISCUSSION. *Paratrogomys whistleri* is a primitive, small, mesodont heteromyid rodent. It might be placed among the Mioheteromyinae, except that it shows incipient development of the p4 X-pattern that characterizes the Perognathinae (and Dipodomyinae). In reality, the Perognathine X-pattern is incompletely developed in modern *Perognathus* Maximilian, 1839 (and *Chaetodipus* Merriam, 1889), as well as in Miocene species assigned to the genus *Perognathus*. The X-pattern is most visible in well-worn individuals and infrequent in unworn or slightly worn individuals. Perhaps the most distinctive feature characterizing Perognathinae (and Mioheteromyinae) is mesodont height of crown, which distinguishes (more or less) these groups from the higher crowned Dipodomyinae.

Whistler (1984) described and illustrated a p4 (UCR 10419) and P4 (UCR 21182) from the Boron Fauna, assigning these specimens to *Trogomys* cf. *T. rupinimentae*. These heteromyids from the Boron Fauna are near the smaller limit of the size range of *Paratrogomys whistleri* from the Crowder Formation; however, the protolophid of the p4 in the Boron specimen is oriented obliquely relative to the metalophid. This feature suggests the Boron specimens are related to *Trogomys* rather than *Paratrogomys*.

Korthomys new genus

Mookomys (part) Wood, 1935:80–92, fig. 8.
"*Mookomys*" Sutton and Korth, 1995:287–288, fig. 9F.

TYPE AND INCLUDED SPECIES. *Mookomys formicorum* Wood, 1935.

DIAGNOSIS. The same as for species until further species are described.

DISTRIBUTION AND AGE. Lower part of the Harrison Formation, Nebraska (Wood, 1935; Arikareean NALMA); Anceney Fauna, Montana (Sutton and Korth, 1995; Barstovian NALMA); and Barstow Formation, California (Lindsay, 1972; Barstovian NALMA).

ETYMOLOGY. Named for William W. Korth in recognition of his numerous contributions to the fossil history of rodents.

DISCUSSION. *Korthomys* differs from *Mookomys* Wood, 1931 (*fide* Korth, 1997:36) by having lower crown height, weakly developed lophodonty and near absence of cingula. *Korthomys* differs from *Paratrogomys* gen. nov., *Mioheteromys* Korth, 1997, and *Proheteromys*

Table 1 Measurements of teeth (mm.). **ABBREVIATIONS: O.R.** = observed range; **V** = coefficient of variation.

Tooth		n	Mean ± SD	V	O.R.
Paratrogomys whistleri					
p4	Length	9	0.95 ± 0.077	8.1	0.76–1.00
	Width	9	0.96 ± 0.0916	9.5	0.83–1.08
m1	Length	10	1.04 ± 0.0618	5.9	0.95–1.15
	Width	11	1.19 ± 0.0642	5.4	1.09–1.29
m2	Length	13	0.99 ± 0.0624	6.3	0.90–1.075
	Width	13	1.20 ± 0.0721	6	1.05–1.29
m3	Length	7	0.81 ± 0.0304	3.8	0.76–0.93
	Width	7	0.94 ± 0.0486	5.2	0.86–1.21
P4	Length	17	1.18 ± 0.0915	7.8	1.00–1.33
	Width	17	1.29 ± 0.0573	4.4	1.20–1.42
M1	Length	14	0.95 ± 0.0572	6	0.83–1.02
	Width	15	1.29 ± 0.0418	3.2	1.26–1.39
M2	Length	12	0.89 ± 0.0788	8.9	0.71–0.98
	Width	12	1.24 ± 0.0921	7.4	1.00–1.35
M3	Length	5	0.82 ± 0.0654	8	0.75–0.90
	Width	5	0.98 ± 0.134	13.7	0.83–1.175
Korthomys formicarum					
p4	Length	1	1		
	Width	1	1.01		
m1	Length	2	1.04		1.00–1.08
	Width	1	1.22		
m2	Length	1	0.93		
	Width	2	1.19		1.11–1.26
P4	Length	1	1.4		
	Width	1	1.33		
M1	Length	1	0.925		
	Width	1	1.42		
M3	Length	2	0.835		0.83–0.84
	Width	1	1.17		
Mioheteromys crowderensis					
p4	Length	11	1.00 ± 0.0891	8.9	0.81–1.12
	Width	11	0.99 ± 0.0918	9.3	0.80–1.10
m1	Length	8	1.04 ± 0.078	7.5	0.89–1.12
	Width	6	1.25 ± 0.0939	7.5	1.08–1.32
m2	Length	5	0.94 ± 0.0669	7.1	0.88–1.04
	Width	5	1.15 ± 0.0394	3.4	1.09–1.18
m3	Length	3	0.79 ± 0.0557	7.1	0.73–0.84
	Width	3	0.94 ± 0.052	5.5	0.89–0.98
P4	Length	8	1.27 ± 0.122	9.6	1.12–1.425
	Width	8	1.31 ± 0.0623	4.8	1.20–1.40
M1	Length	4	1.00 ± 0.00	0	1
	Width	4	1.31 ± 0.115	8.8	1.22–1.48
M2	Length	3	0.86 ± 0.052	6	0.80–0.89
	Width	3	1.15 ± 0.0578	5	1.08–1.18
M3	Length	1	0.72		
	Width	1	1.08		
Proheteromys sulculus					
p4	Length	6	1.01 ± 0.0785	7.7	0.92–1.13
	Width	6	1.01 ± 0.0483	4.75	0.92–1.06
m1	Length	4	0.99 ± 0.0278	2.8	0.97–1.03
	Width	4	1.13 ± 0.105	9.3	1.03–1.275
m2	Length	3	0.99 ± 0.101	10.2	0.88–1.08
	Width	6	1.13 ± 0.0551	4.9	1.07–1.21
m3	Length	4	0.83 ± 0.0503	6.1	0.76–0.88
	Width	3	0.95 ± 0.0265	2.8	0.92–0.97
P4	Length	3	1.23 ± 0.085	6.9	1.20–1.44
	Width	4	1.29 ± 0.0499	3.9	1.24–1.34

Table 1 Continued.

Tooth		n	Mean ± SD	V	O.R.
M1	Length	0			
	Width	2	1.41		1.37–1.44
M2	Length	3	0.95 ± 0.0306	3.2	0.92–0.98
	Width	2	1.32		1.28–1.36
M3	Length	1	0.88		
	Width	1	1.04		

Wood, 1932, in having bunodont cheek teeth with cusps robust and inflated. Upper incisors, cranial, and postcranial features of *Korthomys* are unknown.

Korthomys formicarum (Wood, 1935) new combination

Figures 4 and 5

Mookomys formicorum Wood, 1935:80–92.
Mookomys formicarum Reeder, 1956:135.
Mookomys cf. *M. formicorum* Lindsay, 1972:42–45.
"*Mookomys*" cf. "*M.*" *formicarum* Sutton and Korth, 1995:287–288.
Mookomys formicarum Korth, 1997:37.

LECTOTYPE. CM 10178, right P4, from the lower Harrison Formation about 2 miles NE of Agate, Ne (Wood, 1935:89). This taxon is based on *Mookomys formicorum* Wood (1935), the holotype of which—CM 10177, right M1 (described as right m1)—has been missing since the mid-1950s. CM 10178, along with CM 10179 (right m2) and CM 10177, was described by Wood (1935) as the hypodigm from ant hills in lower Harrison Formation. The lectotype was selected from the topotypic material of the species, although the best available sample of specimens (13 of 17 isolated cheek teeth) is primarily from the Barstow Formation; the topotypic material of the species is recognized as

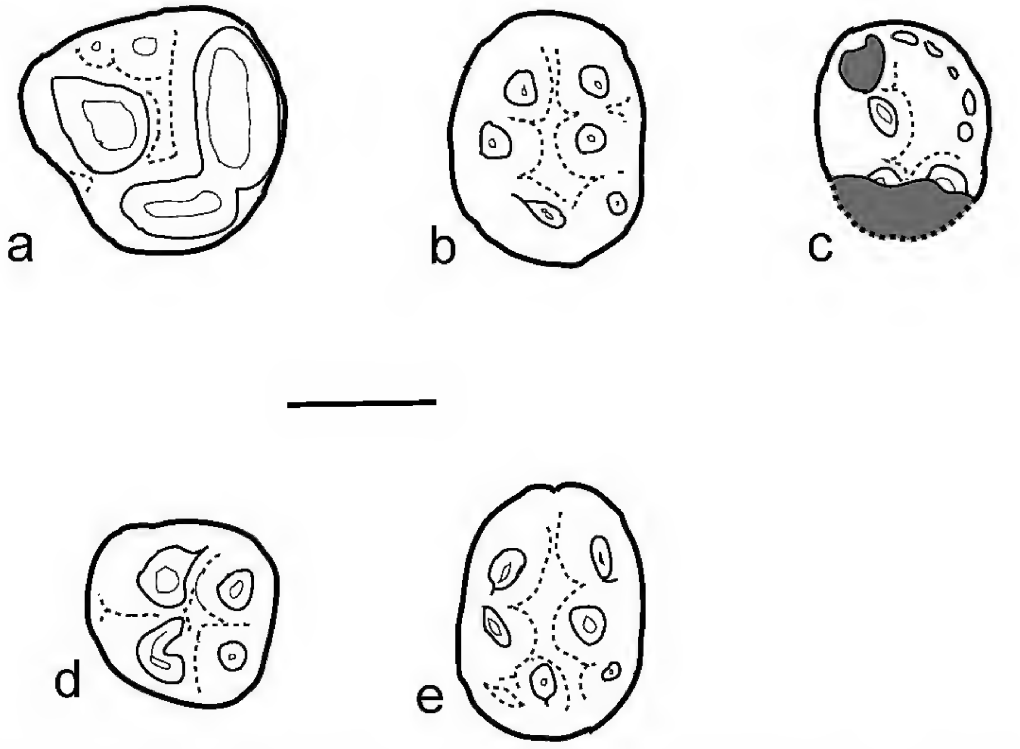

Figure 4 Line drawings of *Korthomys formicarum* gen. nov. Occlusal view of isolated cheek teeth: **a**, L1816-3087, left P4; **b**, L1816-2898, right M1; **c**, L1816-3120, partial left M3; **d**, L1816-2949, right p4; **e**, L1816-2901, left m2. Scale bar = 1 mm.

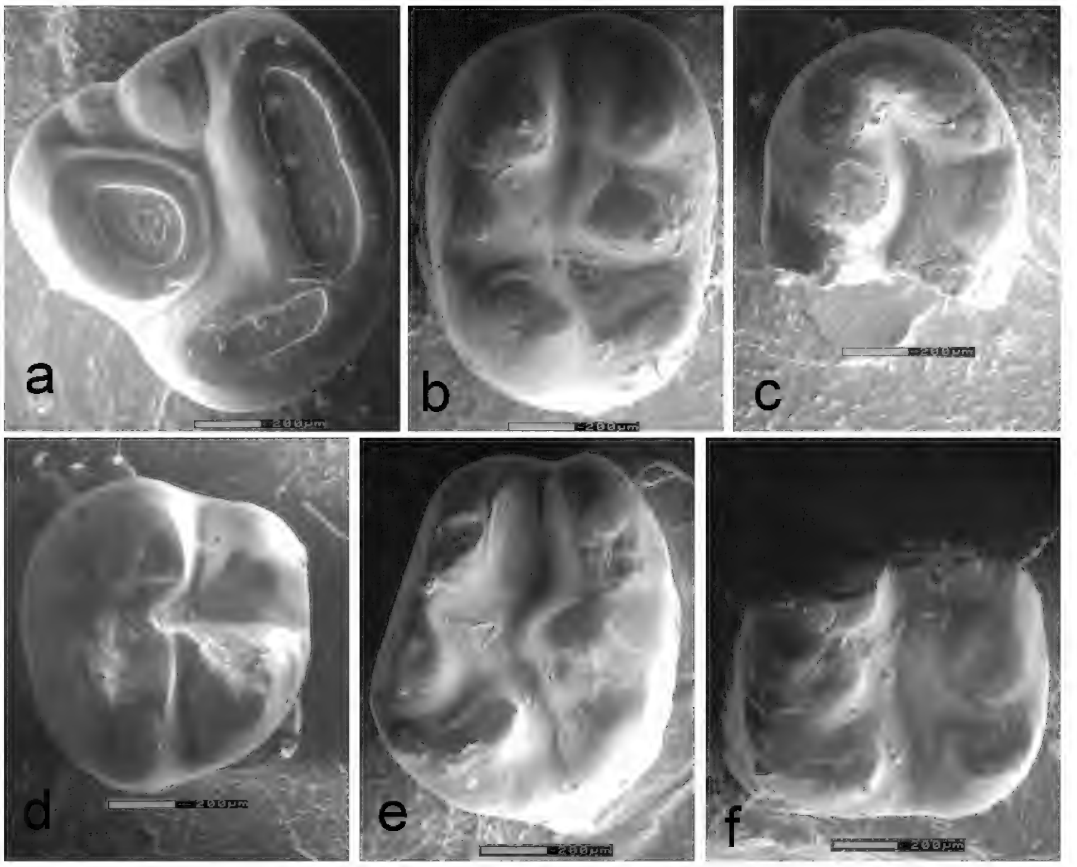

Figure 5 SEM photos of *Korthomys formicarum* gen. nov. Occlusal view of isolated cheek teeth (**a–e** same specimens as in Fig. 4): **a,** left P4; **b,** right M1; **c,** partial left M3; **d,** right p4; **e,** left m2; **f,** L1585-2950, partial left m1. Scale bars = 200 μm.

Arikareean NALMA, whereas all of the remaining materials (15 isolated cheek teeth) are from Barstovian deposits. Known only from the type species, *Korthomys formicarum* (Wood).

REFERRED SPECIMENS. Thirteen isolated cheek teeth from the Barstow Formation, Southern California: UCMP 77042, left M1; UCMP 77045, right M2; UCMP 77043, left m1; UCMP 78555, right m1; UCMP 77146, left m2; SBCM L1816-2898, right M1; SBCM L1816-2900, left m2; SBCM L1816-2901, left m2; SBCM L1816-2949, right p4; SBCM L1816-2950, left m1; SBCM L1816-3087, left P4; SBCM L1816-3120, left M3; and SBCM L1816-3121, right m1.

DIAGNOSIS. Small, low-crowned rodent with inflated, bunodont cusps; cranial, postcranial, and incisor characters unknown.

p4. With central enamel pit and narrow protolophid oriented subparallel to metalophid; lophids joined labial to center by protostylid and hypoconid.

Lower molars. Bilophate, joining both centrally and labially after moderate wear; anterior cingulum weakly developed (m1 and m2) or absent (m3).

P4. Protoloph with a large protocone and a small isolated paracone; metaloph J-shaped, with subequal metacone, hypocone, and large entostyle.

Upper molars. U-shaped (M1 and M2) with lingual union of protoloph and metaloph, or D-shaped (M3), with both lingual and labial union of protoloph and metaloph.

DISTRIBUTION AND AGE. Lower part of the Harrison Formation (Arikareean NALMA), Nebraska; Anceney Fauna, Montana (Barstovian NALMA); and Barstow Formation, California (Barstovian NALMA).

DESCRIPTION. Small rodent with bunodont cheek teeth and inflated cusps.

p4. With central enamel pit; protolophid slightly narrower than, and aligned subparallel relative to, metalophid; lophids joined labial to center after early wear by closely appressed protostylid and hypoconid; with four distinct cusps, hypoconid slightly larger than subequal metaconid and protostylid, protoconid the small-

est cusp; union of metaconid and hypoconid after early wear, followed by union of protoconid and protostylid with more wear; transverse valley offset at midline, shallow and displaced posteriorly labial to midline, deep and displaced anteriorly lingual to midline.

m1. Bilophate, with lophids joining centrally and labially after moderate wear; four subequal cusps (protoconid, metaconid, entoconid, and hypoconid) plus two (or three) smaller protostylid and hypostylid (hypostylid may be multicusped); protostylid placed slightly posterior relative to protoconid; anterior cingulum on anterolabial corner of tooth, joining protostylid.

m2. Smaller than m1; remnant of anterior cingulum is less distinct than in m1; hypostylid indistinct, and initial union of lophs is central, between the protoconid and hypoconid.

m3. Smaller than m2, with small metaconid and protoconid on metalophid, indistinct entoconid and hypoconid on hypolophid; stylar cusps absent on low labial cingulum.

P4. Protoloph with prominent protocone and small, isolated paracone having a low anterior spur; metaloph with three large cusps (metacone, hypocone, and entostyle), forming a J-shaped metaloph; the protocone is isolated until late wear, expanding anterolabially with wear; a hypostyle is absent.

M1. Incompletely bilophate with the protoloph slightly wider than the metaloph; lophs joined lingually after moderate wear by union of the protostyle and hypostyle; six prominent cusps with the paracone and protostyle placed slightly anterior relative to the protocone on the protoloph, and the metacone and hypostyle placed slightly anterior relative to the hypocone on the slightly curved metaloph; the hypostyle is slightly twinned and larger than the protostyle.

M2. Similar to M1 although smaller size, with transverse valley less deep and the hypostyle smaller than the protostyle.

M3. Small, with D-shaped occlusal outline; paracone, protocone, and protostyle on the protoloph, a minute metacone, hypocone, and multicusped hypostyle on the metaloph; lophs united lingually and labially after early wear to form a shallow central lake.

Measurements of *Korthomys formicarum* are given in Table 1.

DISCUSSION. Korth (1997:37) removed this species from the genus *Mookomys* after discussing the relationship of *Mookomys formicarum* with other species of *Mookomys*, explaining, "It is impossible to assign '*M.*' *formicarum* to any currently recognized genus of heteromyid." *Mookomys* was placed in the new subfamily Mioheteromyinae by Korth (1997), characterized (in part) by union of p4 lophids labial to the center of the tooth and poorly developed (or retained) enamel pit in the trigonid of p4.

These features are recognized on *Korthomys*, thereby linking it with the known Mioheteromyinae. Another feature of the Mioheteromyinae, characterized by Korth (1997), is lingual union of the lophs on P4. Lophs on the P4 of *Korthomys* are not united until very late wear, with the protocone expanding anterolabially rather than lingually as wear proceeds. This delays union with the large lingual entostyle, although initial union of the lophs will likely be lingual. This feature seems unique to *Korthomys*, although it resembles the occlusal wear seen in some members of the Florentiamyidae of Wahlert (1983). Wahlert (1983) characterized Florentiamyidae on the basis of derived cranial and dental characteristics; unfortunately, cranial material of *Korthomys* is currently unknown. Cheek teeth of Florentiamyidae are also rather bunodont with low, inflated cusps. However, the premolars of florentiamyids are usually large relative to their molar teeth; the P4 of *Korthomys* has accessory cusps on the protoloph but none of the known florentiamyids have cusp morphology similar to that of *Korthomys*.

Mookomys cf. *M. formicarum* (Wilson, 1960) from the Hemingfordian Quarry A Fauna in Colorado was referred to the probable Harrymyine *Stratimus strobeli* (Korth et al., 1990). Another species of *Mookomys*, *M. thrinax* (Sutton and Korth, 1995) from the Barstovian Anceney Fauna in Montana, shows some similarity to primitive Heteromyinae or possibly to Harrymyinae.

Another potential relative of *Korthomys* is the geomyoid genus *Tenudomys* Rensberger (1973), described as a pleurolicine Geomyidae from Arikareean deposits in Oregon. Korth (1993) reviewed the genus *Tenudomys*, placing it in Geomyoidea, *incertae sedis*, with inferred position near the stem of Heteromyidae and Geomyidae, based primarily on cranial characters (e.g., enlarged optic foramen; fused buccinator, masticatory, and accessory foramen ovale; and alisphenoid expanded dorsally). Korth (1993) placed the material described as *Mookomys*(?) *bodei* Wilson (1949) from the Arikareean NALMA part of the Sespe Formation in Southern California in *Tenudomys*, along with material described as *Tenudomys* by Rensberger (1973; that is, *Tenudomys macdonaldi*) from the Sharps Formation of South Dakota (Arikareean NALMA), plus *Tenudomys dakotensis* MacDonald (1963) also from the Sharps Formation and *Tenudomys basilaris* Korth (1989) from the Brule Formation (Orellan NALMA) of South Dakota.

Tenudomys resembles *Korthomys* in having brachydont cheek teeth with robust cusps and weak, but persistent, cingula. The p4 of *Tenudomys* retains four isolated cusps until late wear, as in *Korthomys*, and P4 of *Tenudomys basilaris* (illustrated in Korth, 1993:fig. 2g) has a small, isolated paracone, similar to *Korthomys formi-*

carum, although other species of *Tenudomys* lack such an isolated cusp. If derived from *Tenudomys*, then *Korthomys* would represent a very primitive but rare and long-lived relative. Because of this uncertainty, *Korthomys* is placed in Heteromyidae, *incertae sedis*. Relationships of the intriguing rodent *Korthomys* remain unresolved.

Mioheteromys Korth, 1997

The subfamily Mioheteromyinae was characterized by Korth (1997) on the basis of cranial and dental features, noting that mioheteromyines have brachyodont to mesodont cheek teeth, with union of p4 lophids labial to the midline, union of P4 lophs lingually, and usually an enamel pit in the center of p4. Korth (1997) identified two genera with sulcate upper incisors among the Mioheteromyinae: *Mookomys* and *Mioheteromys*.

We recognize three genera of mesodont heteromyid rodents in the Mojave Desert region—*Paratrotrogomys*, *Mioheteromys*, and *Proheteromys*—each with sulcate upper incisors. We recognize three discrete "morphs" among the sulcate upper incisors in this sample, distinguished as follows: morph 1 (long and narrow) is associated with the holotype of *Paratrogomys whistleri*; morph 2 (short and wide), with a shallow "step" in the anterior surface, is associated with a skull fragment bearing P4 of *Proheteromys sulculus*; morph 3 (long and wide), with a deep "step" in the anterior surface, is assigned to *Mioheteromys crowderensis* sp. nov. Note that direct association of sulcate upper incisors associated with cheek teeth of *M. crowderensis* is not firmly established; we assign sulcate upper incisors with morph 3 to *M. crowderensis* primarily because dissociated cheek teeth of *M. crowderensis* occurred with an upper incisor of morph 3 in blocks of sediment from the Crowder Formation. Also, teeth of *M. crowderensis* are arguably the second most common small rodent recorded from the Crowder Formation, after *P. whistleri*.

We place *Mioheteromys*, along with the other mesodont heteromyids in this study, within the subfamily Heteromyidae *incertae sedis* because of current uncertainty regarding phyletic relationships within these Miocene heteromyid rodents.

Mioheteromys crowderensis new species

Figures 6 and 7

Peridiomys sp. Lindsay, 1972:58, 1995:362, fig. 3.

HOLOTYPE. SBCM L1585-1523, right dentary with p4 and m1–3 from SBCM locality 1.103.125 (PS-1, Quarry A).

HYPODIGM. Holotype plus 27 referred specimens from the lower part of the Crowder Formation: L1585-1427, right P4; L1585-1459, right p4; L1585-1491, right dentary with i1 and p4; L1585-1492, right maxilla with P4, M1–3, plus left m3; L1585-1493, left m2; L1585-1494, i1 fragment; L1585-1497, right dentary with i1, p4, and m1; L1585-1503, right m1 and m2; L1585-1512, left P4; L1585-1513, right P4; L1585-1514, right P4; L1585-1515, left M2; L1585-1517, right M1; L1585-1518, right M1; L1585-1519, right M1; L1585-1520, right m1; L1585-1521, right M2; L1585-1522, left p4 and m1–2; L1585-1524, right i1 and p4; L1585-1525, left p4 and m1–2; L1585-1529, right i1 and p4; L1585-1530, left p4; L1585-1531, left p4; L1585-1532, left p4; L1585-1535, left m1; L1585-1537, right m1; L1585-1540, right m3. Six isolated teeth from the Barstow Formation: L1816-2959, left P4 (loc. UALP 8905); L1816-2960, left P4 (loc. UALP 8905); L1816-3122, left P4 (loc. UALP 9009); L1816-3123, right P4 (loc. UALP 9009); UCMP 78170, P4 (loc. V-6605); and UCMP 78172, left P4 (loc. V-66153).

DISTRIBUTION AND AGE. Crowder Formation, Bed 1 (SBCM 1.1003.125), Bed 3 (SBCM 1.103.130), and Bed 19 (SBCM 1.130.139), San Bernardino County, California (late Hemingfordian and early Barstovian NALMAs); Barstow Formation (UCMP localities V-6605 and V-66153 and UALP localities 8905 and 9009), San Bernardino County, California (Barstovian NALMA).

DIAGNOSIS. Small rodent with mesodont cheek teeth and sulcate upper incisors; dentary with massive masseteric ridge extending below and anterior to p4; lower incisors with well-rounded enamel surface of narrow width; upper incisors relatively long and narrow, with deep "step" separating levels on anterior surface (= morph 3), enamel relatively thick.

p4. Protolophid narrow, usually oriented oblique relative to metalophid; protolophid and metalophid unite after moderate wear by low and narrow loph labial to center of tooth.

Lower molars. Bilophate, lophids of subequal width, with metalophid flexed labially (J-shaped) and slightly higher than the straight hypolophid, lophids unite centrally and labially after moderate wear (m1) or unite initially on labial side then centrally (m2).

m3. Retains a minute hypostylid (and wide hypolophid); posterior cingulum and posteroconid absent.

P4. With large entostyle oriented anteroposteriorly on lingual side of tooth, placed anterior relative to the metaloph, producing lingual union of the protoloph and metaloph after early wear; protocone elongated transversely and usually lacking an accessory cuspule; metacone placed slightly anterior relative to hypocone on the metaloph; hypostyle absent.

Upper molars. Bilophate with lophs of subequal width and height, unworn protoloph straight, metaloph rounded lingually (J-shaped), labial and lingual cusps of both lophs placed

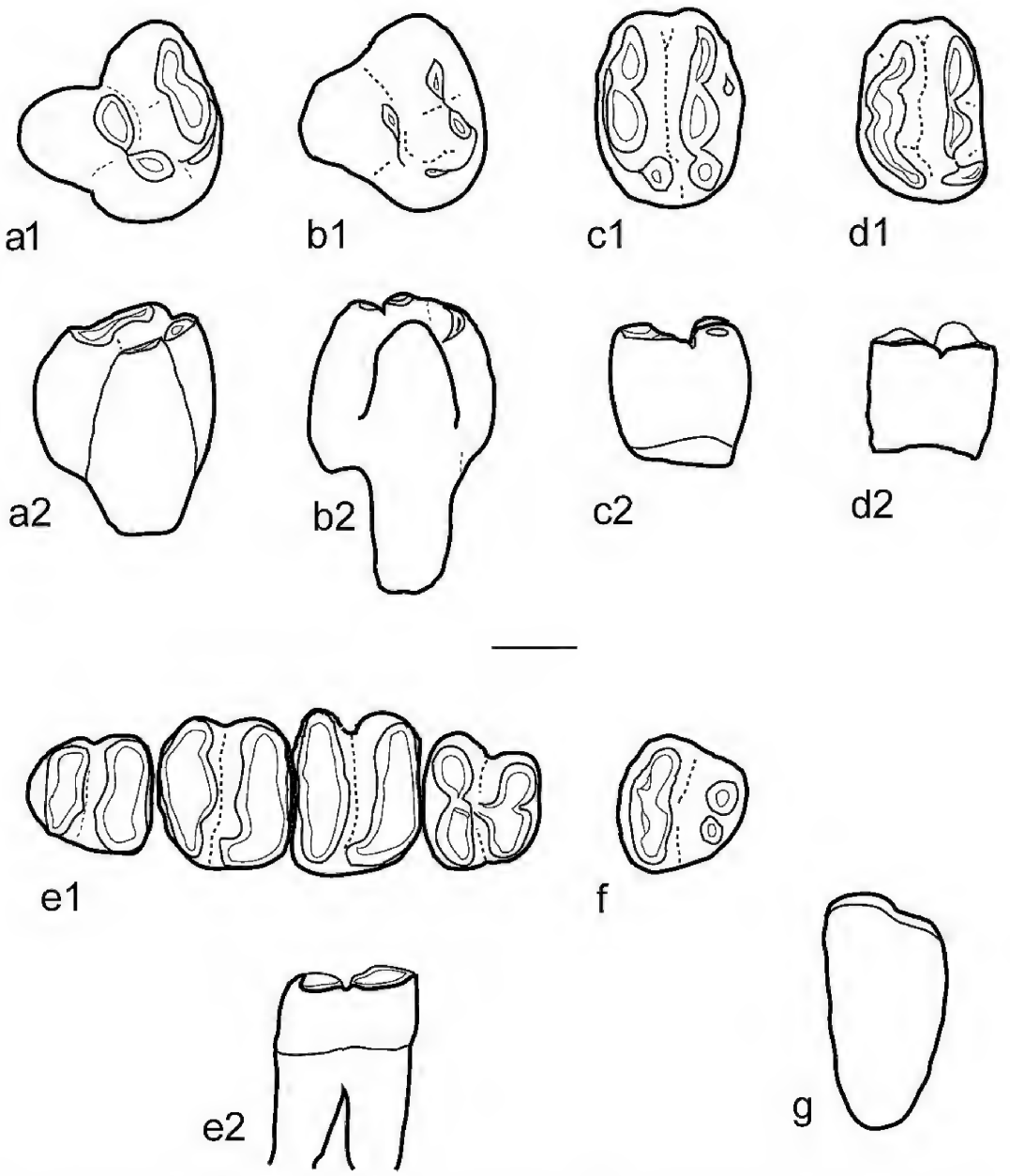

Figure 6 Line drawings of *Mioheteromys crowderensis* n. sp.: **a,** L1816-2960, left P4: **a1,** occlusal view; **a2,** anterior view; **b,** L1585-1512, left P4: **b1,** occlusal view; **b2,** anterior view; **c,** L1585-1519, right M1: **c1,** occlusal view; **c2,** lingual view; **d,** L1585-1521, right M2: **d1,** occlusal view; **d2,** lingual view; **e,** HOLOTYPICAL SPECIMEN L1585-1523, right p4–m3: **e1,** occlusal view; **e2,** right m1, labial view; **f,** L1585-1524, right p4, occlusal view; **g,** L1585-1494, cross section of upper incisor. Scale bar = 1 mm.

slightly anterior relative to medial cusps (protocone and metacone), lophs unite lingually after moderate wear, anterior cingulum discontinuous, usually represented by a minute cuspule anterior to and between the paracone and protocone.

Mioheteromys crowderensis is smaller than *Mioheteromys amplissimus* Korth (1997) and *Mioheteromys agrarius* (Klingener, 1968); it is similar in size to *Mioheteromys arcarius* (Korth, 1996), differing from that species in having slightly larger molar teeth and a greater tendency for central union of lophids in lower molars.

Mioheteromys crowderensis is similar in size to species of *Balantiomys* (Korth, 1997), differing

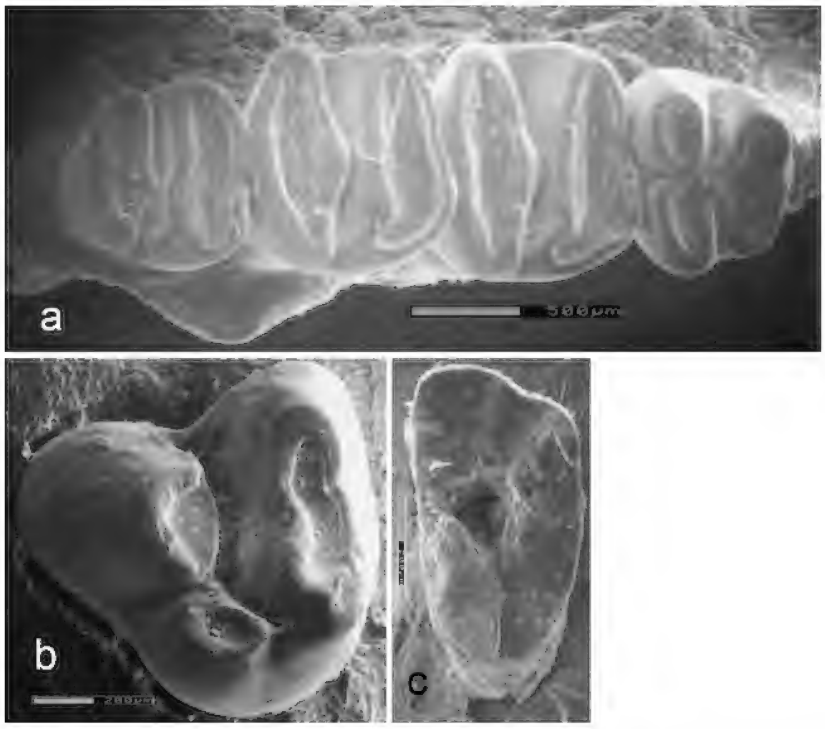

Figure 7 SEM photos of *Miobeteromys crowderensis* sp. nov.: **a,** HOLOTYPICAL SPECIMEN L1585-1523, occlusal view of right p4–m3 (as in Fig. 6e1); **b,** L1816-2960 occlusal view of left P4 (as in Fig. 6a1); **c,** L1585-1494 cross section of upper incisor (as in Fig. 6g). Scale bars: a = 500 μm; b, c = 200 μm.

from them in having sulcate upper incisors. *Miobeteromys crowderensis* differs from *Paratrogomys whistleri* in having p4 with the protolophid oriented obliquely relative to the metalophid; it differs from *Korthomys* in having higher crowned and less robust cheek teeth; it differs from *Probeteromys sulculus* Wilson (1960) in having lower molars with lophids that usually unite centrally rather than labially.

ETYMOLOGY. Crowder, in reference to the source deposit of the species, plus the suffix *-ensis* (Latin), denoting a place.

DESCRIPTION. Upper incisors are relatively long and narrow, sulcate, with a deep "step" labial to the midline that separates levels on the anterior surface of the incisor (morph 3); lower incisors with well-rounded anterior enamel surface; masseteric ridge massive, extending anterior to position of p4; mental foramen placed well in advance of masseteric ridge.

p4. Protolophid narrower than metalophid and usually oriented obliquely (~10–15°) relative to the metalophid (protostylid and hypoconid closer on labial side of tooth); protolophid joins the metalophid slightly labial to the midline after moderate wear by a low and narrow loph; central enamel pit poorly developed; four principal cusps (protoconid, protostylid, metaconid, and hypoconid), with the protostylid smaller than the protoconid; the metalophid is relatively wide but all of the available specimens are too worn to identify presence (or absence) of a minute hypostylid on the labial end of the metalophid.

m1. Bilophate, with the metalophid and hypolophid of equal (or near-equal) width and the metalophid slightly higher than the hypolophid; lophids unite after moderate wear, usually both centrally and labially; metalophid rounded at anterolabial corner of the tooth (J-shaped); hypolophid straight, with hypostylid aligned with the hypoconid and entoconid; four prominent cusps with both the metalophid (protoconid and metaconid) and the hypolophid (hypoconid and entoconid) cusps elongated transversely and joined after early wear; protostylid and hypostylid small, with protostylid slightly higher than the hypostylid; protostylid partially blocks the transverse valley; anterior cingulum low, joining protostylid and anterior protoconid; posterior cingulum and posteroconid absent.

m2. Slightly smaller than m1, with metalophid and hypolophid uniting initially on labial side of tooth after moderate wear; other characters as in m1.

m3. Smaller than m2, with hypolophid slightly narrower (transversely) than metalophid; lophids

unite centrally, labially, and lingually after moderate wear; hypostylid small but distinct; other characters as seen in m2.

P4. Lingual union of unworn protoloph and metaloph (after early wear) by a narrow loph that joins the large entostyle and lingual protocone; secondary medial union of lophs by protocone and hypocone in late wear; protoloph lower than metaloph, with protocone elongated transversely and lacking distinct accessory cuspules; entostyle large and robust, higher than protoloph, located anterior relative to the metaloph, joining the posterior cingulum posteriorly; hypostyle absent; metacone usually placed slightly anterior relative to the hypocone; hypocone elongated transversely, joining metacone after early wear; posterior cingulum short, flexed, joining entostyle and posterolingual side of metacone.

M1. Bilophate, with protoloph subequal to width of metaloph; unworn lophs of subequal height; lophs unite lingually after early wear; protoloph straight, metaloph flexed anteriorly on lingual end (J-shaped); labial and central cusps elongated transversely, united after early wear; labial cusps (paracone and metacone) and especially the lingual cusps (protostyle and hypostyle) placed slightly anterior relative to the central cusps (protocone and hypocone); protostyle and hypostyle joined on lingual side of tooth after early wear; anterior cingulum discontinuous, usually represented by a minute cuspule between and anterior to the paracone and protocone; posterior cingulum low and narrow, joining the hypostyle posteriorly or continuing labially to join the metacone.

M2. Slightly smaller than M1, with protoloph slightly wider than the metaloph; posterior cingulum narrow and discontinuous, joining the hypostyle and lingual hypocone; other characters as seen in m1.

M3. No securely identified specimens.

Measurements of *Mioheteromys crowderensis* are given in Table 1.

DISCUSSION. This taxon was described as *Peridiomys* sp. by Lindsay (1972, 1974) on the basis primarily of the lingual union of the P4 lophs in a small mesodont heteromyid. It is likely that more records of this taxon can be identified from the Barstow Formation, now that its dental features are more securely defined with material from the Crowder Formation. Korth (1997) distinguished *Peridiomys* Matthew 1924 from *Balantiomys* Korth (1997) on the basis, in part, of size of the p4 protolophid cusps (protoconid twice as large as protostylid in *Peridiomys*, these cusps subequal in *Balantiomys*); it is unlikely that *Peridiomys* was recorded in sediments of the Barstow Formation, but a thorough review of the material from there might turn up unrecognized specimens of *Balantiomys*.

Mioheteromys crowderensis seems most similar to *Mioheteromys arcarius* (Korth, 1996, 1997), recorded from the Bijou Hills Fauna of South Dakota and the Wood Mountain Fauna of Saskatchewan (Storer, 1975). Both the Bijou Hills and the Wood Mountain faunas are Barstovian NALMA. *Mioheteromys crowderensis* is also difficult to differentiate from *Proheteromys sulculus* (see below).

Proheteromys sulculus Wilson, 1960
Figures 8–10

HOLOTYPE. KU 10203, left dentary with p4–m2 from Quarry A in the Pawnee Creek Formation, Logan County, Colorado (Hemingfordian NALMA).

REFERRED SPECIMENS. 32 specimens: L1585-135, left m3; L1585-147, left p4; L1585-149, right M2; L1585-311, left M2; L1585-312, left M2; L1585-314, right m1; L1585-315, left m1; L1585-316, left m2; L1585-398, right m1; L1585-497, right p4; L1585-549, right P4; L1585-583, right m1; L1585-742, left M1; L1585-743, right M3; L1585-744, left m1; L1585-1171, right p4; L1585-1403, left m3; L1585-1430, right P4; L1585-1457, left p4; L1585-1463, right p4; L1585-1487, right m2; L1585-1488, left m2; L1585-1490, left m3; L1585-1507, left P4; L1585-1509, right P4; L1585-1511, left P4; L1585-1528, left p4; L2148-155, left m2; L2148-156, right M1; L2148-163, left m3; L2148-164, right m2; L2148-165, right m2.

DISTRIBUTION AND AGE OF REFERRED SPECIMENS. Lower part of the Crowder Formation (beds 1–17), San Bernardino County, Southern California (late Hemingfordian NALMA).

DESCRIPTION. Upper incisors relatively short anteroposteriorly and wide (morph 2), with a shallow "step" located lateral to the midline separating levels of the anterior surface.

p4. Central enamel pit usually absent or poorly developed, present in one (SBCM L1585-1528) of five specimens; protolophid narrower than metalophid, commonly oriented obliquely (10–15°) relative to the metalophid, with labial cusps (protostylid and hypoconid) much closer than lingual cusps (protoconid and metaconid); union of protolophid and metalophid after moderate wear labial to middle of tooth (three of five specimens) or on midline by narrow low loph (one of five specimens); protoconid and protostylid united anteriorly (two specimens) or posteriorly (two specimens) after early wear; minute mesoconid between protoconid and protostylid in two of five specimens; minute hypostylid present on labial end of metalophid; no posteroconid.

m1. Bilophate, with J-shaped metalophid parallel and slightly higher than straight hypolophid; transverse width of metalophid and hypolophid subequal; lophids unite initially after moderate

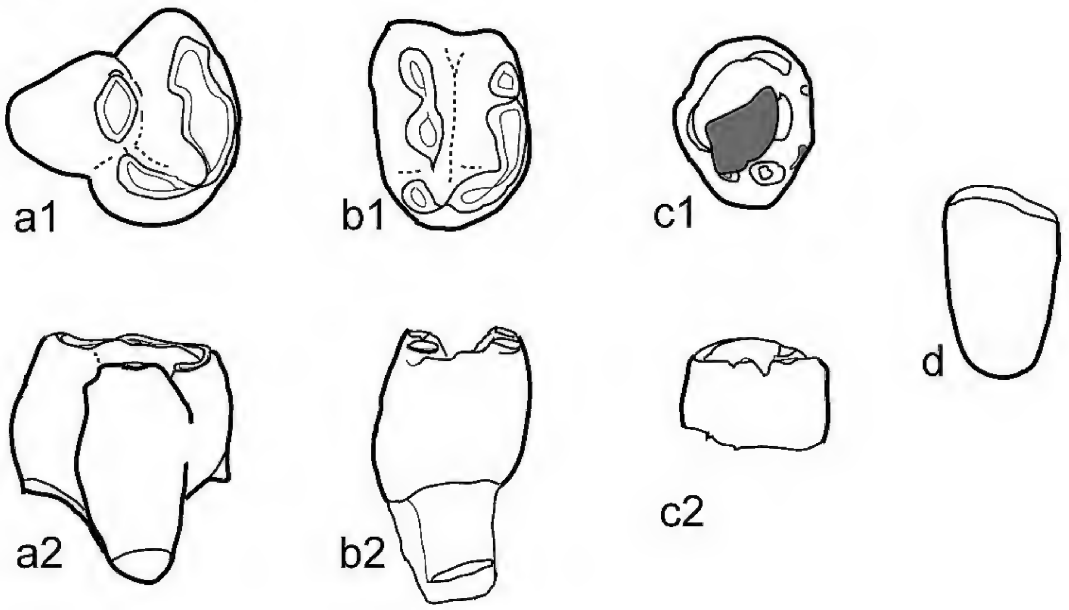

Figure 8 Line drawings of *Proheteromys sulculus* Wilson, upper dentition: **a,** L1585-1511, left P4: **a1,** occlusal view; **a2,** anterior view; **b,** L1585-312, left M2: **b1,** occlusal view; **b2,** lingual view; **c,** L1585-743, right M3: **c1,** occlusal view; **c2,** lingual view; **d,** L1585-549, cross section of upper incisor. Scale bar = 1 mm.

wear, by protostylid and hypostylid, on labial side of the tooth, followed by central union of lophids (protoconid and hypoconid) in late wear; four prominent, subequal cusps (protoconid and metaconid on the metalophid, hypoconid and entoconid on the hypolophid) elongated transversely and united after early wear; protostylid small, elongate anteroposteriorly, placed posterior relative to protoconid and partially blocking transverse valley; hypostylid small and circular, placed labial to hypoconid; anterior cingulum prominent, flexed at anterolabial corner of tooth, joining anterior side of protoconid near midline; posterior cingulum and posteroconid absent.

m2. Smaller than m1; hypostylid much lower and smaller than protostylid; other characters as seen in m1.

m3. Smaller than m2; transverse width of hypolophid narrower than metalophid; protostylid minute or indistinct; hypostylid absent; anterior cingulum short and low; other characters as in m2.

P4. Lingual union of protoloph and metaloph after moderate wear by short, narrow loph that joins the large entostyle with the protocone; central union of protocone and hypocone only after late wear; protoloph much lower than metaloph, with protocone elongate transversely (slightly compressed anteroposteriorly); indistinct remnant of a minute accessory cuspule on two of five specimens; entostyle large but not inflated, oriented almost perpendicular to metaloph; hypostyle absent; metacone placed slightly anterior relative to hypocone and joining protocone after early wear; shallow posterolabial inflection between hypocone and metacone.

M1. Bilophate, transverse width of protoloph and metaloph subequal; protoloph straight, metaloph rounded near posterolingual corner (J-shaped), slightly lower height than protoloph; lophs subparallel, joined lingually after early wear by union of protostyle and hypostyle; lophs joined centrally in late wear; prominent cusps on lophs elongated transversely and joined after early wear; protostyle and hypostyle subequal in size with hypostyle slightly higher and placed slightly anterior relative to the hypocone, partially blocking the transverse valley; anterior cingulum discontinuous, usually represented by a small, isolated cuspule anterior to and between the paracone and protocone; posterior cingulum low, uniting hypostyle, hypocone, and metacone after early wear.

M2. Smaller than M1; protoloph slightly wider than the metaloph; anterolabial remnant of anterior cingulum absent; other characters as seen in M1.

M3. D-shaped occlusal outline; lophs unite lingually and labially after early wear; protoloph straight, metaloph well rounded; prominent paracone and protocone, minute but distinct

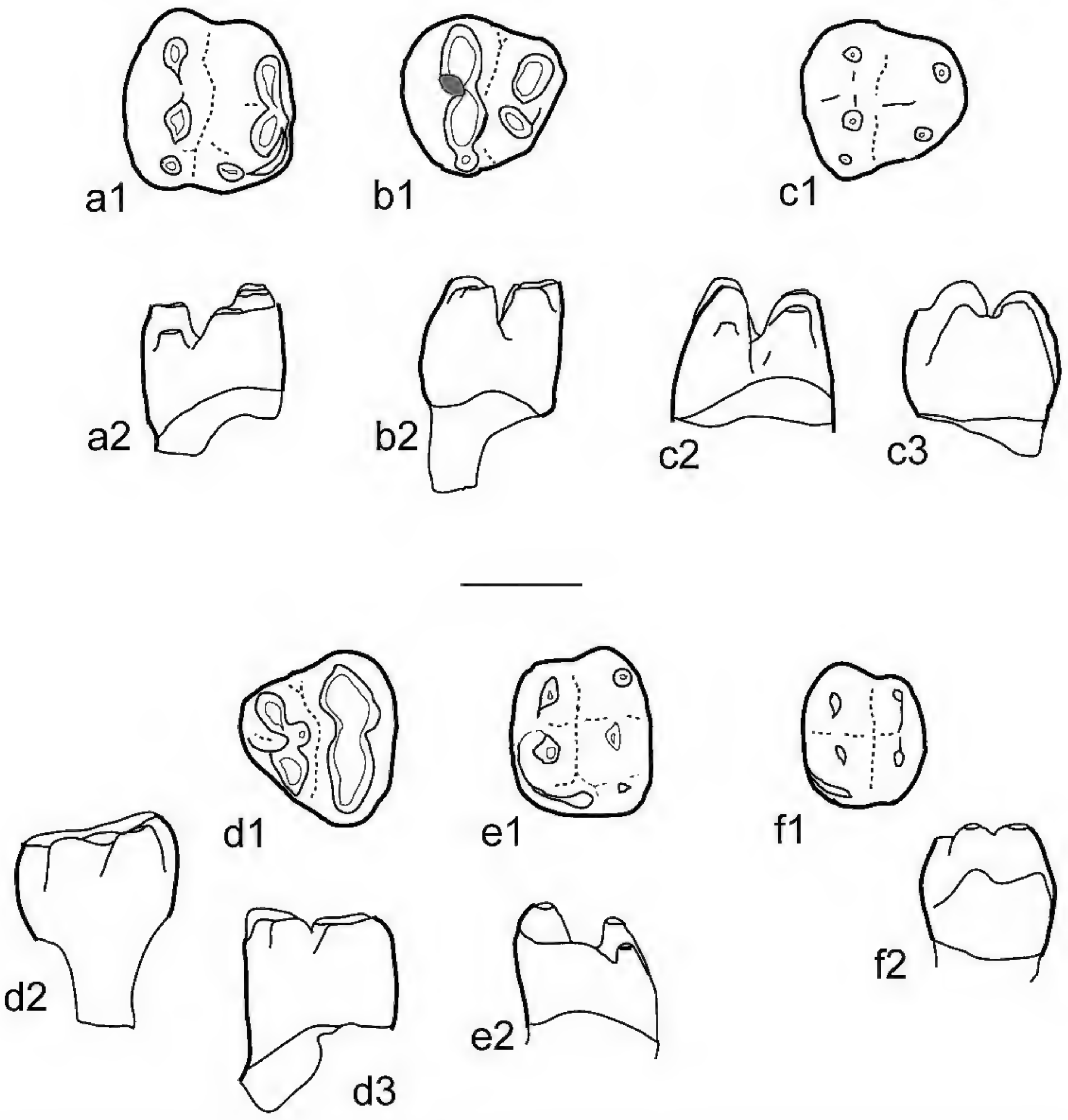

Figure 9 Line drawings of *Proheteromys sulculus* Wilson, lower cheek teeth: **a,** L1585-314, right m1: **a1,** occlusal view; **a2,** labial view; **b,** L1585-1171, right p4: **b1,** occlusal view, **b2,** labial view; **c,** L1585-497, right p4: **c1,** occlusal view; **c2,** labial view; **c3,** anterior view; **d,** L1585-147, left p4: **d1,** occlusal view; **d2,** anterior view; **d3,** labial view; **e,** L1585-316, left m2: **e1,** occlusal view; **e2,** labial view; **f,** L1585-1490, left m3: **f1,** occlusal view; **f2,** posterior view. Scale bar = 1 mm.

protostyle and hypostyle, indistinct paracone and metacone; anterior cingulum discontinuous, posterior cingulum continuous, enclosing a shallow central basin.

Measurements of *Proheteromys sulculus* are given in Table 1.

DISCUSSION. The genus *Proheteromys* Wood (1932) is a complex and poorly characterized taxon. Korth (1997) noted problems with the taxonomic distinction of *Proheteromys* but failed to address that complexity. We agree with Korth's assessment and second the proposal that *Proheteromys magnus* Wood (1935) and *Proheteromys maximus* James (1963) should probably be removed from the genus *Proheteromys*, but assigning those species to another genus is beyond the limits of this study. Similarly, *Proheteromys cejanus* Gawne, 1975, has an asulcate upper incisor, so it should also be assigned to a different genus.

Proheteromys sabinensis Albright, 1996, is comparable in size to *Proheteromys sulculus*, but *P. sabinensis* lacks a protostylid on p4, and its P4 occasionally has an accessory cuspule lingual

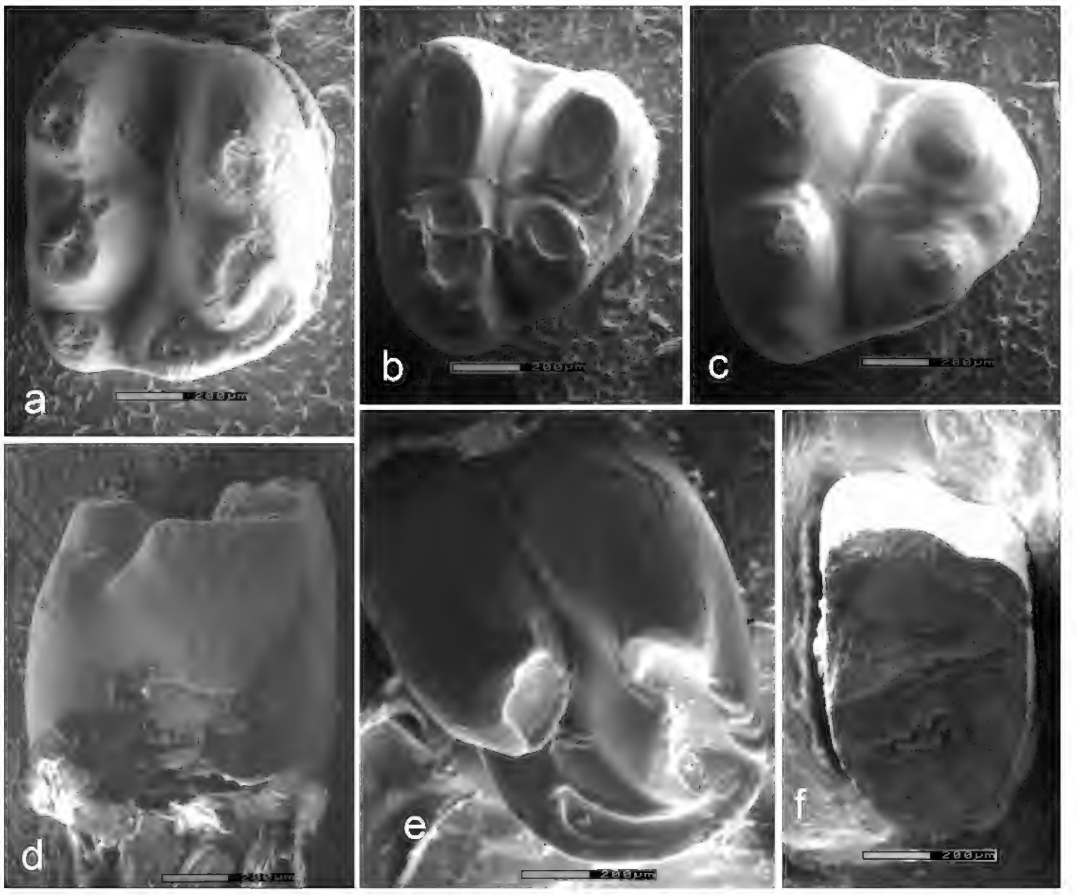

Figure 10 SEM photos of *Proheteromys sulculus* Wilson: **a,** L1585-314, occlusal view of right m1 (as in Fig. 9a1); **b,** L1585-1171, occlusal view of right p4 (as seen in Fig. 9b1); **c,** L1585-497, occlusal view of right p4 (as seen in Fig. 9b1); **d,** L1585-314, labial view of right m1 (as seen in Fig. 9a2); **e,** L1585-1511, occlusal view of left P4 (as seen in Fig. 8a1); **f,** L1585-549, cross section of upper incisor (as seen in Fig. 8d). Scale bars = 200 μm.

to the protocone (Albright, 1996). As noted by Wilson (1960), *Proheteromys floridanus* Wood, 1932, is smaller than *P. sulculus*.

Interestingly, Wilson (1960:76–77) noted the variable presence of accessory cusps (anteroconid and hypostylid) on the p4 of *P. sulculus* in the sample from Quarry A; we note the presence of a minute hypostylid in unworn or slightly worn p4s (Fig. 9b1 and 9c1) but no distinct anteroconid in the samples from Crowder and Barstow formations. Also, Wilson (1960:77) noted that the absence of accessory tubercles on the p4 of *Proheteromys matthewi* (Wood, 1935) distinguishes it from *P. sulculus*. We note that illustration of the holotypical specimen (AMNH 12896a) of *P. matthewi* by Wood (1935:fig. 96a) looks very similar to *Mioheteromys crowderensis*, and if this specimen were recorded from the Crowder Formation it would easily be assigned to *M. crowderensis*. Actually, *P. matthewi* should probably be considered a *nomina dubius* until more material of *P. matthewi* is reported from its stratotype, the upper Rosebud Formation of South Dakota, and the genus *Proheteromys* is better understood. *Proheteromys sulculus* is smaller than *Proheteromys magnus*, *Proheteromys maximus*, and *Proheteromys toledoensis* Albright, 1996.

The material assigned to *Proheteromys sulculus* (Lindsay, 1974) in the Vedder Fauna from the Branch Canyon Formation (Santa Barbara County, California) should be assigned to a different, unnamed species of *Proheteromys*, in that the material from the Branch Canyon Formation is distinctly larger than the material assigned to *P. sulculus* from the Crowder and Barstow formations and from the Quarry A Fauna in Colorado.

MESODONT HETEROMYID DENTITION

Modern heteromyids are either mesodont or hypsodont, although extant species of *Pero-*

Table 2 Korth index of crown height.

Specimen	Element	Length	Width	Height	K index
Paratrogomys whistleri					
1412	Lm1	0.95	1.25	0.5	0.4
1412	Rm1	1	1.21	0.5	0.41
1413	Rm1	1	1.21	0.53	0.44
1431	Rm1	1.08	1.18	0.52	0.44
1432	Rm1		1.29	0.52	0.4
1447	Rm1	1	1.17		
1465	Lm1	1.15	1.26	0.55	0.48
1466	Lm1	1.075	1.15	0.55	0.48
1467	Lm1	0.98	1.11	0.5	0.45
1468	Rm1	1.1	1.21	0.59	0.49
1469	Lm1	0.92	1.12	0.94	0.39
1471	Rm1	1	1.2	0.456	0.38
		K index (mean) = 4.76/11 = 0.43			
Mioheteromys crowderensis					
1497	Rm1	1.12	1.32		
1503	Rm1	0.96	1.2	0.48	0.4
1520	Rm1	1.08	1.27	0.36	0.28
1522	Rm1	1.01	1.32		
1523	Rm1	0.89	1.08	0.33	0.31
1525	Lm1	1.08			
1535	Lm1	1.08			
1537	Rm1	1.08	1.3	0.44	0.34
		K index (mean) = 1.33/4 = 0.33			
Proheteromys sulculus					
314	Rm1	0.97	1.1	0.33	0.3
315	Lm1	1.03	1.275	0.42	0.33
398	Rm1	0.98	1.03	0.33	0.32
583	Rm1	0.975	1.1	0.42	0.38
744	Lm1				
		K index (mean) = 1.33/4 = 0.33			

gnathus and *Chaetodipus* are frequently called brachyodont or brachydont. Miocene heteromyids show varying degrees of increasing crown height, but they have previously been difficult to evaluate. Korth (1997:table 2) introduced a clever technique similar to the method of Barnosky (1986) to calibrate relative crown height in Miocene heteromyids. This method is based on the ratio of crown height (from the base of the enamel to the notch of the transverse valley on the labial side of the tooth) to the transverse width of p4 and m1. We tried this method, finding it difficult to repeat measurements on p4 but getting fairly consistent results on m1. We believe this ratio of crown height to transverse width of posterior loph (ht/trp) in lower molars provides a reliable measure of crown height in these rodents, and call it the "Korth crown height index." For consistency, and reliability, we recommend this index be applied only to the lower m1, and we suggest that whenever possible, both the occlusal and labial side of a heteromyid m1 should be illustrated, to provide direct evaluation of this crown height measure. It is possible that application of this index to other teeth (e.g., M1 and m2) might be applied if m1 is not available, but such application should only accompany similar measurements from a large sample of securely identified teeth. A short summary of m1 "Korth index" crown height for mesodont heteromyids described here is presented in Table 2. Note that *Mioheteromys crowderensis* and *Proheteromys sulculus* have about the same crown height, whereas *Paratrogomys whistleri* is slightly higher crowned according to these measurements.

We believe the reason that p4 crown height is so variable relates to the difficulty in determining crown height in teeth with a gradual slope in the transverse valley. That is, on p4, if the transverse valley has a very sloping surface, the crown height might be measured from the lowest level of the transverse valley (where slope occurs) or from the floor of the transverse valley near the midline of the tooth; these two measurements will give minimum and maximum values for crown height. Therefore, measurements of crown height in m1, which has a distinct notch on the labial surface at the point where the transverse valley terminates (unless worn), are likely to yield more reliable indices for crown height.

Table 3 Heteromyid premolar lophids. Orientation of the lophids (protolophid and metalophid) on 15 species of extant heteromyid rodent were evaluated. Orientations were initially "eye-balled" using magnification of a binocular microscope; later, illustrations and measurements of indeterminate premolars were made.

	Subparallel	Slightly oblique (<15°)	Oblique (>15°)	Total
Chaetodipus penincillatus	15	0	5	20
C. intermedius	16	0	3	19
C. baileyi	12	0	8	20
C. hispidus	5	0	0	5
C. formosus	3	0	0	3
Total	53	0	16	69
Perognathus flavus	21	0	0	21
P. amplus	16	0	3	20
P. goldmani	4	0	1	5
P. longimembris	5	0	0	5
P. fallax	4	0	1	5
P. californicus	0	0	1	1
P. nelsoni	4	0	0	4
P. apache	4	0	1	5
P. arenarius	3	0	0	3
P. artus	4	0	1	5
Total	64	0	8	72
Grand total	117	0	24	141

Another measure we have applied to evaluate heteromyid dental morphology is the orientation (subparallel or oblique) of p4 lophids. Note that we have characterized p4 of *Paratrogomys* with subparallel lophids and p4 of *Mioheteromys crowderensis* and *Proheteromys sulculus* with oblique lophids. The type (KU 10203) of *P. sulculus* from the Quarry A Fauna in northeastern Colorado has p4 with subparallel orientation of the protolophid and metalophid; however, two of the illustrated specimens (KU 10217 and KU 10225) in the hypodigm of *P. sulculus* have p4 with oblique orientation of these lophids (Wilson, 1960:figs. 110 and 112). We have found these lophids are usually oriented between 10° and 15° in *P. sulculus* from the Crowder Formation. We consider that any lophid orientation greater than about 10° is oblique.

A short survey was conducted on modern species of *Perognathus* and *Chaetodipus* in the mammal collection of the University of Arizona to evaluate the frequency of this feature in modern heteromyid rodents. An initial survey of lophid orientation in modern heteromyids showed high variability of this measure, so a more rigorous study was made on 10 species of *Perognathus* and five species of *Chaetodipus*, with results shown in Table 3. Our results indicate that several levels of variability occur within modern heteromyid species; in general, species of *Perognathus* have less oblique lophids than those of *Chaetodipus*, and in approximately half, or 54%, of the modern specimens examined, a weak (between 3° and 14°) oblique orientation can be recognized in p4 lophids. In one species (*Chaetodipus baileyi* Merriam, 1894), about 40% of the p4 lophids are oriented more than 15°; in another species (*Perognathus amplus* Osgood, 1900), about 15% of the p4 lophids are oriented more than 15°. It appears to us that oblique orientation of p4 lophids is very common in modern heteromyid rodents, and it can be used to characterize heteromyid dentitions, but, like other morphological characters, orientation of p4 lophids must be applied, along with a number of other features, on large samples when making taxonomic interpretations.

We assume that oblique orientation of the p4 lophids is an inheritable trait that permits species with that trait greater opportunity to grind, and thereby consume, seeds of variable size. Functionally, this results in narrowing (and partially closing) the labial side of the p4 transverse valley, thereby "holding" a seed between the protolophid and metalophid of the p4 before crushing it with the blunt protocone of the P4. We note a similar oblique orientation of the protoloph and the metaloph on P4 of the heteromyid genus *Harrymys* Munthe (1988) that also occurs during Hemingfordian NALMA. Perhaps oblique orientation of upper premolar lophs in this genus provides selective advantage to "hold" seeds of an optimum size for crushing with the blunt protolophid of *Harrymys*. This, of course, is speculative, but it provides a rationale for interpreting why the oblique orientation of lophs and lophids in fossil heteromyids is a useful trait that might have positive selection in some heteromyid populations.

CONCLUSIONS

1. Four heteromyid rodents, including two new species, are described and characterized on the basis of their dental features. Relationships between these species are still poorly known because cranial features which help to characterize many groups of small geomyid rodents are unknown or poorly established for these four species. Consequently, they are all designated Heteromyidae *incertae sedis*.
2. The first new taxon, *Paratrogomys whistleri* gen. et sp. nov., is a small mesodont rodent, very similar to modern species of *Perognathus*, the pocket mouse. Like the pocket mouse, it has a narrow sulcate upper incisor, p4 with four cusps, the posterior cusps (metacond and hypoconid) of which unite after early wear to form a metalophid, and with anterior cusps oriented subparallel to the metalophid; the P4 has a large, central, single-cusped protoloph that joins the wide metaloph centrally and lingually, and the metaloph lacks a hypostyle. *Paratrogomys whistleri* differs from species of *Perognathus* by having a p4 that lacks central union of the protolophid and metalophid, and the metalophid has a minute hypostylid; also, the P4 often has a minute accessory cusp on the protoloph, with broader and more lingual union of the protoloph and metaloph. *Paratrogomys whistleri* is known only from the Crowder Formation in Southern California.
3. The second new taxon, *Korthomys formicarum* comb. nov. is based on the species *Mookomys formicarum*; a new genus is named and a lectotype designated because the holotype of *M. formicarum* has been missing for about 60 years. *Korthomys formicarum* differs from the other rodents described in this study by having lower crowned, bunodont, cheek teeth with inflated cusps. *Korthomys* resembles members of the extinct Florentiamyidae. In florentiamyids the premolars are commonly larger than the molar teeth; however, the p4 of *K. formicarum* is noticeably smaller than m1, although P4 is slightly larger than M1. Incisor, cranial, and postcranial features of *K. formicarum* are unknown. *Korthomys formicarum* is known from the Barstow Fauna in Southern California, the Anceney Fauna in Montana, and the lower Harrison Fauna in Nebraska.
4. The third new taxon, *Mioheteromys crowderensis* sp. nov., is similar in crown height (mesodont) and size to *Paratrogomys whistleri*. It also has a sulcate, or stepped, upper incisor, like *P. whistleri*, but the sulcus is slightly greater in *M. crowderensis*. *Mioheteromys crowderensis* differs from *P. whistleri* in having the p4 protolophid oriented obliquely relative to the metalophid, and the P4 protoloph joins the metaloph lingually via a large entostyle, rather than centrally. The material described as *Peridiomys* sp. from the Barstow Formation by Lindsay (1972) is placed in *M. crowderensis*. *Mioheteromys crowderensis* is currently known from both the Crowder and Barstow formations in Southern California.
5. The fourth rodent taxon, *Proheteromys sulculus*, is similar in size and height of crown to both *Paratrogomys whistleri* and *Mioheteromys crowderensis*; it also has a sulcate upper incisor, but the incisor of *P. sulculus* has a smaller step (or sulcus) than either *P. whistleri* or *M. crowderensis*. In addition, *P. sulculus* is similar to *M. crowderensis* (and differs from *P. whistleri*) in having the p4 protolophid oriented obliquely relative to the metalophid, and the P4 protoloph joins the metaloph lingually rather than centrally. Cheek teeth of *P. sulculus* are distinguished from *M. crowderensis* on the basis of several subtle differences, such as, slightly larger size, lingual union of lophs in upper premolars and molars, and labial union of lophids in lower molars. *Proheteromys sulculus* is known from the lower part of the Crowder Formation in Southern California and the Quarry A Fauna in northeastern Colorado. The material described as *P. sulculus* from the Vedder Fauna by Lindsay (1974) should be assigned to another species.
6. Korth (1997) recognized a primitive radiation of Miocene heteromyid rodents on the basis, in part, of genera and species that had been assigned previously to the extant subfamilies Perognathinae, Dipodomyinae, and Heteromyinae. The four species described in this contribution demonstrate some of the diversity of that Miocene radiation and support renewed analysis of small, mesodont heteromyid species to better understand the evolution of this diverse and successful family.
7. Toward that goal, we support use of the "Korth index" (ratio of crown height from the notch of the transverse valley on the labial side of the tooth to the transverse width of the tooth) applied to the m1 as a useful standard for characterizing relative crown height in heteromyid rodents.
8. We also suggest that orientation of the p4 protolophid relative to the metalophid is a useful dental feature for characterizing and differentiating species of mesodont heteromyid rodents, as applied in this contribution.

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Biostratigraphy of the Miocene Crowder Formation, Cajon Pass, southwestern Mojave Desert, California

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ABSTRACT. The Crowder Formation in Cajon Pass, San Bernardino County, California, is located on the southwestern margin of the Mojave Desert. This formation contains fossil vertebrates, including abundant small mammals, which have been recovered from a sequence of more than 20 paleosol horizons. The stratigraphic sequence reflects three local faunas representing early Miocene, each of which is proposed here as new: the Wye Local Fauna and the Squaw Peak Local Fauna (late Hemingfordian Land Mammal Age) and the Sulfur Spring Local Fauna (early Barstovian Land Mammal Age). A fourth local fauna, not formally named and which is stratigraphically higher, contains small mammals representing the middle part of the Hemphillian Land Mammal Age. The three local faunas representing the transition from the Hemingfordian to Barstovian land mammal ages clarify the age of deposition of the Crowder Formation and allow biostratigraphic comparisons to other Miocene Mojave Desert faunas.

INTRODUCTION

The Crowder Formation is located in the southwestern Mojave Desert Province of Southern California (Fig. 1). Crowder Formation sediments have been exposed in Cajon Pass (Fig. 2) by headward erosion along Cajon Creek, a drainage that is rapidly capturing the headwaters of the Mojave River. Cajon Pass is at the junction of the Pacific Plate and the North American Plate. Interaction between these tectonic plates has elevated the San Gabriel Mountains to the west of Cajon Pass and the San Bernardino Mountains to the east. This uplift has exposed 70 million years of sedimentary section, including the late Cretaceous marine San Francisquito Formation (Kooser, 1985; Lucas and Reynolds, 1991), the Oligocene to early Miocene marine Vaqueros Formation (Woodring, 1942), and early Miocene through Pleistocene continental deposits (Woodburne and Golz, 1972; Woodburne, 1991a). The extreme local tectonism caused the Transverse Ranges (San Gabriel Mountains and San Bernardino Mountains) to reach their maximum height of more than 10,000 feet by less than 500,000 years ago. This geologic textbook is within easy reach of researchers and students, at the intersection of Interstate Highway 15 and Highway 138 in southwestern San Bernardino County.

METHODS AND MATERIALS

Paleontological monitors collected fossils of large mammals from the Crowder Formation (Reynolds, 1983, 1992) during excavation for the construction of Highway 138 by the California Department of Transportation and along railroad cut exposures in the upper Crowder Formation units. Realizing the fossiliferous potential of Crowder Formation paleosols, a standard sample (6,000 pounds; Society for Vertebrate Paleontology, 1995) was collected from each Hemingfordian and Barstovian age paleosol that was encountered by the highway excavation and at other paleosols within the section. More than 9,409 diagnostic fossils were recovered from 167,000 pounds of paleosol matrix and assigned San Bernardino County Museum (SBCM) number L1585, indicating a loan of specimens from the San Bernardino National Forest. Paleosols in the lower part of the Crowder Formation were numbered sequentially and designated paleosol "beds." Twenty sampled paleosols in the sequence of beds 1 to 23 were assigned SBCM locality numbers SBCM 1.103.54 and SBCM 1.103.125 through 1.103.144.

ABBREVIATIONS

Ba Barstovian North American Land Mammal Age

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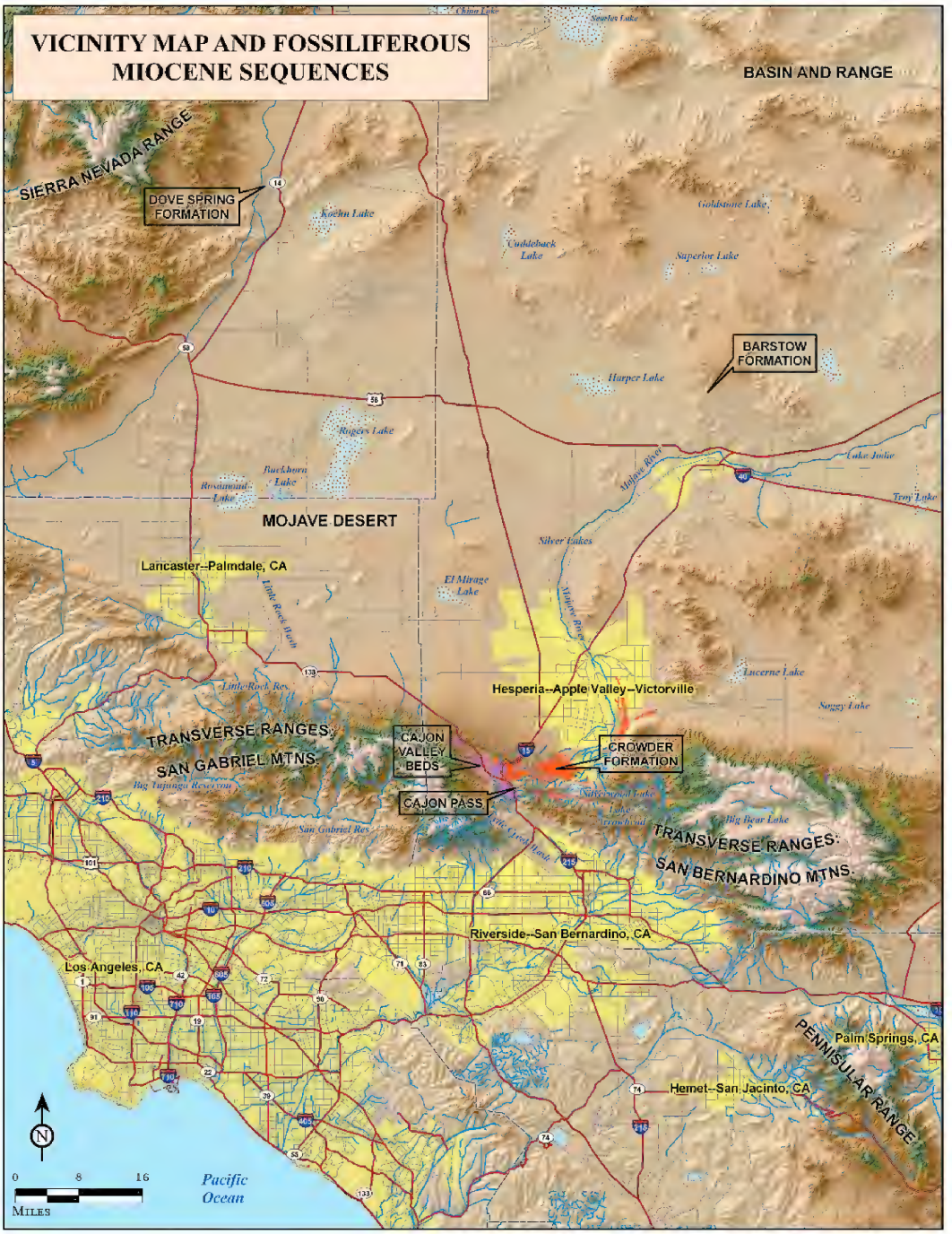

Figure 1 Vicinity map and selected fossiliferous Miocene sequences in Southern California.

Cl	Clarendonian North American Land Mammal Age		reversals in the Earth's magnetic field
GPTS	Geomagnetic polarity time scale: A chronology based on the sequence of	He	Hemingfordian North American Land Mammal Age

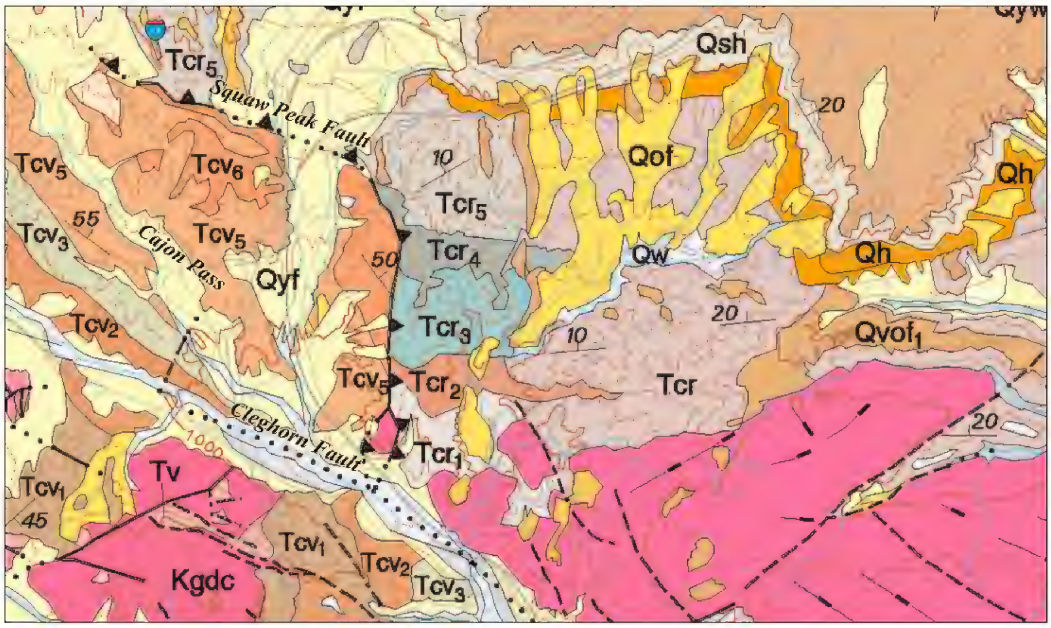

Figure 2: Geologic map showing the Crowder Formation in the Cajon Pass area (USGS Geologic Map: San Bernardino 30' x 60' Quad, Morton and Miller, 2003).

Qyf	Young alluvial-fan deposits (Holocene and late Pleistocene)
Qof	Old alluvial-fan deposits (late to middle Pleistocene)
Qsh	Shoemaker Gravel (Pleistocene)
Qh	Harold Formation (Pleistocene)
Qw	Very young wash deposits (late Holocene)
$Qvof_1$	Very old alluvial-fan deposits, Unit 1 (early Pleistocene)
Tcr	Crowder Formation (Pliocene and Miocene)
Tcr_5	Crowder Formation, Unit 5 (Pliocene)
Tcr_4	Crowder Formation, Unit 4 (Pliocene and Miocene)
Tcr_3	Crowder Formation, Unit 3 (Pliocene and Miocene)
Tcr_2	Crowder Formation, Unit 2 (Pliocene and Miocene)
Tcr_1	Crowder Formation, Unit 1 (Pliocene and Miocene)
	Cajon Valley Formation (Miocene)
Tcv_6	Cajon Valley Formation, Unit 6
Tcv_{5a} → Tcv_5	Cajon Valley Formation, Unit 5, includes reddish-brown conglomerate unit (Tcv_{5a})
Tcv_4	Cajon Valley Formation, Unit 4
Tcv_3	Cajon Valley Formation, Unit 3
Tcv_2	Cajon Valley Formation, Unit 2
Tcv_1	Cajon Valley Formation, Unit 1
Tv	Vaqueros Formation (Miocene and Oligocene)
Kgdc	Biotite granodiorite, Cajon area (Cretaceous)

Figure 2 Geologic map showing the Crowder Formation and the Squaw Peak Fault, Cajon Valley, San Bernardino County, California.

Hh	Hemphillian North American Land Mammal Age
LF	Local fauna: an aggregate of fossil vertebrate species that has a limited distribution in time from closely grouped localities in a limited geographic area; a local fauna could be based on taxa from a single locality (see Woodburne, 2004b:Definitions)
NALMA	North American Land Mammal Age
SBCM	San Bernardino County Museum, Redlands, California USA

DEFINITIONS

Unit

In this paper, we follow the convention of previous geologic mapping (Foster, 1980; Weldon, 1984, 1985) that subdivides the Crowder Formation into five mappable units. The term "Unit" may approximate the term "Member," as used in the Code of Stratigraphic Nomenclature. A Crowder Formation "Unit" is limited in areal extent, Units 1 to 4 extending laterally a little

more than a mile. Therefore, the term as used during previous mapping suggests that a unit is a mappable subdivision of a stratified sedimentary sequence smaller and more limited in areal extent than a Member of a sedimentary formation.

Bed

A bed is a subdivision of a stratified sedimentary sequence that is smaller than a unit. It is herein used to describe a red-brown paleosol bed developed on the surface of a stabilizing pulse of fluvial deposition. Twenty-three paleosol beds were sampled for vertebrate fossils within the Crowder Formation. See the paleosol description in Woodburne and Golz (1972).

Geologic Provinces

A geologic province is a region characterized by similar geologic features, structure, and history. Distinct faunal compositions recognized in specific geographic areas (faunal provinciality) have been recognized across the North American continent (Barnosky, 1986; Tedford et al., 2004). Faunal distinction persists through time, suggesting it is in part controlled by, or maintained within, regional geologic provinces. Geologic structural provinces (Tedford et al., 2004) that contain faunal sequences that pertain to the Crowder Formation fauna include the following:

The Northern Great Basin Province consists of Nevada, Utah, Arizona, and the eastern portion of California. A recognized subprovince is the Mojave Desert of western Nevada and California.

The California Coast Range Province lies to the west of the Northern Great Basin Province. Two of the four subprovinces west of the Mojave Desert Province are the Transverse Ranges and the Peninsular Ranges. Sediments of the Crowder Formation were derived from sources in a Miocene Mojave Desert Province. Today, the Crowder Formation is located north of the San Andreas Fault, within the westernmost San Bernardino Mountains of the eastern Transverse Range Province, on its border with the Mojave Desert Province.

The Southern Great Basin Province includes New Mexico, west Texas, and Chihuahua, Mexico.

The Great Plains Province, north of the Southern Great Basin Province, extends from Oklahoma to Saskatchewan.

The Gulf Coast Province extends from eastern Texas through Florida and the Atlantic Coast.

North American Land Mammal Ages

North American Land Mammal Ages (NALMAs) are biochronologic units with boundaries tied to first-appearance datum (as defined by Woodburne, 2004a, with further refinement by Tedford et al., 2004). The following definitions of these land mammal ages are after Tedford et al. (2004) and focus on taxa pertinent to the Crowder Formation sequence.

The Hemingfordian is based on taxa from the Great Plains and Gulf Coast sedimentary sequences. The start of the Hemingfordian NALMA (He) and the early He1 are based on immigrants, including shrews, ochotonids, trogontherine beavers, amphicyonids, hemicyonids, ursids, procyonids, the Mustelinae (*Miomustela*), Teleoceratine and Aceratherine rhinoceros, and the dromomerycid *Aletomeryx*. The earliest appearance of the heteromyid Cupidinimus, as well as certain mylagaulids, borophagines, mustelids, horses, peccaries, oreodonts, protoceratids, and camels, characterize He1. He1 contains the latest occurrence of the rhinoceros *Menoceras*.

The late Hemingfordian is characterized by first appearances, among others, of petauristine flying squirrels, the cricetine *Copemys* (late in the sequence), the rabbit *Hypolagus*, dromomerycids including *Sinclairomeryx*, the large camel *Aepycamelus*, and antilocaprids such as *Merycodus* and *Meryceros*.

The Barstovian is based on taxa from the Miocene sediments of the Mud Hills, northwest of Barstow, California, and 50 miles north–northeast of the Crowder Formation in Cajon Pass. The Barstovian and the early Barstovian (Ba1) are defined by first appearances of the hemicyonine *Plithocyon* and the proboscidean *Zygolophodon*. The early Barstovian contains the last occurrence of the late Hemingfordian (He2) holdover *Cynorca*. The late Barstovian (Ba2) is defined by the first appearance of the gomphotherid proboscideans (not present in the Crowder Formation). Among other first appearances are hedgehogs and the ochotonids *Hesperolagomys* and *Russellagus*. The zapodid *Megasminthus* is known from rare occurrences through late Ba2.

No taxa restricted to the Clarendonian have yet been recognized from the Crowder Formation.

The taxa that characterize the Hemphillian are from sediments of the southern Great Plains. Immigrating taxa are used to mark four phases of the Hemphillian NALMA (Hh1, Hh2, Hh3, and Hh4). The Hh1 is defined by first North American appearance of sloths, the cricetodontine murid *Pliotomodon*, the sigmodontine murid *Paranychonomys*, and the geomyid *Pliosaccomys*, among others. The Hh2 is defined by first appearances of a variety of genera, the loss of many early Hemphillian genera, and the last occurrence of genera such as *Leptarctus* and *Aepycamelus*. The Hh3 is recognized by immigrants such as the sloth *Megalonyx* and the pika *Ochotona* and is characterized by taxa such as the cricetids *Peromyscus* and *Onychomys*, the sigmo-

dontines *Calomys* and *Prosigmodon*, and the heteromyid *Prodipodomys*. The defining taxa for the final phase of the Hemphillian (Hh4) include, among others, the leporine *Lepoides*, the gopher *Thomomys* (*Plesiothomomys*), and the cricitines *Baimomys* and *Repomys*.

GEOLOGY

CHARACTERIZATION OF THE CROWDER FORMATION

The Crowder Formation was named by Dibblee (1967), who applied this name to a sequence of fluvial sediments of Pliocene age in the Cajon Pass. An expanded description by Woodburne and Golz (1972) of the Crowder Formation included a re-evaluation of its age and notice that it contained paleosols and was unconformably deposited upon the Cajon Valley Beds. Foster (1980) divided the Crowder Formation into five units and provided detailed work on source areas and paleocurrent direction. He described Unit 1 as pink-orange arkosic sediments; Unit 2 as drab-colored arkosic wacke; Unit 3 as a pale orange, resistant, cliff-forming arkose; Unit 4 as mudstone and siltstone interfingering with arkosic wacke; and Unit 5 as white arkosic sands. These deposits are not exposed in laterally continuous sequences. If they were, the units (Foster, 1980; Weldon, 1984, 1985) probably would have been designated as formal members of the Crowder Formation.

Subsequent workers (Weldon et al., 1981; Weldon, 1985; Meisling and Weldon, 1989) redefined the age of the lowest Crowder Formation units on the basis of magnetic polarity that is tied to small mammal assemblages from paleosols (Reynolds, 1984, 1985, 1991a). The Crowder Formation was estimated to span a period of time from greater than 17 Ma to less than 9.5 Ma (Reynolds, 1985, 1991a; Weldon, 1985).

The Crowder Formation is currently considered to be a lithologically distinct formation that is in fault contact with the Cajon Valley Beds (Figs. 1 and 2) and was deposited at a similar time as those beds (Foster, 1980; Weldon, 1985; Reynolds, 1991a; Woodburne, 1991a). The Crowder Formation is nearly 3,000 feet (~915 m) thick, and it lies northeast of and across the Squaw Peak Fault (Fig. 2) from the early Miocene arkosic Cajon Valley Beds, which have been previously identified as being the Punchbowl Formation (Woodburne and Golz, 1972), the Cajon Formation (Meisling and Weldon, 1982, 1989), and the Cajon Valley Beds (Woodburne, 1991a). The Cajon Valley Beds are approximately 9,000 feet (~2,740 m) thick, and they contain fossils suggesting the sediments span portions of the Hemingfordian and Barstovian, perhaps representing a period between 18 and 14 Ma (Reynolds, 1991a; Woodburne, 1991a).

PALEOSOLS IN THE CROWDER FORMATION

The Crowder Formation contains several thin, brown paleosols, each of which represents an accretional fining-upward sequence. Several Crowder Formation paleosols are degradational, in which a disconformity has removed the fining-upward sequence and the underlying arkosic sands were oxidized and stained a red, maroon, or chartreuse color. Paleosols are common in the Cajon Valley Beds as well as the Crowder Formation. Woodburne and Golz (1972) suggested that they are weathering products that developed on fining-upward sequences of aeolian silts that were deposited upon the fluvial arkosic sandstone. Weathering reduced ferromagnesian minerals, feldspar, rock fragments, and organic materials to produce clay minerals, calcium carbonate (caliche kernels), and the hematite and goethite that cause the red colors of the paleosols.

The paleosols are laterally persistent, and their included dense clay minerals have resisted scouring during later erosional events. The paleosols appear to be unstratified because of severe bioturbation. On the basis of studies of recent paleosols in the Mojave and Colorado deserts (Wells et al., 1990, 1993), and realizing that there have been significant climatic changes since Miocene time, each paleosol in the lower part of the Crowder Formation might represent more than 10,000 years of weathering on a stable

Table 1 Crowder Formation stratigraphy, Cajon Valley, San Bernardino County, California. The measured thickness (Total 860+ m) of the Crowder Formation Units 1 to 5 follows the section that was developed (Weldon, 1985) for presenting geomagnetic sample data.

Thickness (m)	Units	Paleosols	Local Faunas
400	Unit 5		
100	Unit 4		
100	Unit 3	CR 4-4	CR 4-4 Local Fauna
90	Unit 2	Beds 19–23	Sulfur Spring LF
30	Upper Unit 1	Beds 16–18	Squaw Peak LF
140	Lower Unit 1	Beds 1–15	Wye Local Fauna

Table 2 Taxa comprising the Wye Local Fauna, Crowder Formation Unit 1, beds 1 to 15, Cajon Valley, San Bernardino County, California.

Hemingfordian taxa	Beds							
	1	2	3	4	5	9	12	15
Deroceras sp.	•							
Helminthoglypta graniticola	•							
Gerrhonotus sp.				•				
Erycinae gen. et sp. nov.				•				
Megasminthus sp. nov. near *M. gladiofex*	•							
Protospermophilus sp.	•							
Archaeohippus mourningi	•							
cf. *Merycodus* sp.	•							
Miomustela sp. nov.	•							
Leptarctus sp. cf. *L. ancipidens*	•							
Procamelus sp.	•	•						
Michenia agatensis	•	•						
Miolabis tenuis	•	•						
Cynorca sp.?	•	•						
Hesperocamelus (*Aepycamelus*) sp.	•	–	•					
Balantiomys crowderensis	•	–	–	–	•			
Menoceras sp.				•				
Parapliohippus carrizoensis	•	•	–	•	–	–	•	•
Paratrogomys whistleri	•	•	•	•	–	–	–	•
Paradomnina relictus	•	•	–	•	–	–	–	•
Mookomys "altifluminus"	•	•	•	–	•	–	–	•
Perognathus furlongi	•	•	–	–	•	•	–	•
Perognathus minutus	•	–	–	–	–	–	–	–
Proheteromys sulculus	•	•	•	•	•	•	•	•
Petauristodon sp. cf. *P. matthewsi*	•	•	–	–	•	–	–	•
Miospermophilus sp. cf. *M. wyomingensis*	•	•	–	•	•	–	–	–
Tamias sp.		•	–	–	–	–	–	–
Plesiosminthus (*Schaubeumys*) sp. near *P. galbreathi*								•

surface. If the paleosols were stable surfaces, with only minor fluvial deposition, then the intervening arkosic units undoubtedly represent intermittent cyclic and repeated pulses of fluvial deposition.

Fossils of small vertebrate animals (both diagnostic and unidentifiable) were found in all of the sampled paleosols, both accretional and degradational, in the lower Crowder Formation units. Fossils in the Crowder Formation include the remains of Miocene small mammals, reptiles, birds, insects, and mollusks. More rare and large mammals (*Cynorca* sp., *Aepycamelus* sp., and *Menoceras* sp.) have been recovered from the coarse arkosic sandstone of Units 1 and 2.

BIOSTRATIGRAPHY

CROWDER FORMATION

The Crowder Formation has been divided into five discontinuous lithostratigraphic units (Foster, 1980; Weldon, 1984, 1985), each of which contains paleosols or siltstone facies (Table 1). This study uses mapping and stratigraphy that is tied to a sequence of paleomagnetic samples (Weldon, 1984) to order the sequence of the paleosol beds that have produced vertebrate fossils. We discuss the taxa that were recovered from three of those units. When these taxa are stratigraphically restricted, we describe them as local faunas and group them into biostratigraphic divisions in an attempt to place them within recognized NALMAs. This study describes as new local faunas (LFs) the Wye LF and Squaw Peak LF (late Hemingfordian NALMA) and the Sulfur Spring LF (early Barstovian NALMA). Higher in the Crowder Formation section, locality CR 4-4 produced taxa (CR 4-4 LF) that appear to represent the middle Hemphillian NALMA. These biostratigraphic divisions are not equivalent to lithostratigraphic units, and they are based on fossils that sometimes span portions of two lithostratigraphic units or are present in only a portion of one lithostratigraphic unit.

The Wye LF includes 30 taxa from paleosol beds 1 to 15 in Crowder Formation Unit 1 (see Table 2). The Squaw Peak LF contains seven taxa from bed 17 in the upper part of Unit 1 of the Crowder Formation (Table 3). The Sulfur Spring

Table 3 Taxa comprising the Squaw Peak Local Fauna, Crowder Formation, upper part of Unit 1, beds 16 to 18, Cajon Valley, San Bernardino County, California.

Early Barstovian taxa	Bed 16	Bed 17	Bed 18
Tamias sp.		•	
Mookomys "altifluminus"		•	
Perognathus furlongi		•	
Proheteromys sulculus		•	
Cupidinimus halli		•	
Copemys tenuis		•	
Sinclairomeryx sp.		•	

LF includes 11 taxa from beds 19, 20, 22, and 23 in the lower part of Unit 2 of the Crowder Formation (Table 4). The fossil vertebrate assemblage from locality CR 4-4 (Table 5), which is in the top of Unit 3, included nine taxa.

Taxonomic change is demonstrated through the stratigraphic sequence of the Crowder Formation (Tables 4, 6, 7). Taxa that are exclusive to the Wye LF (Table 2) include mollusks, lizards, a boa, a shrew, two mustelids, a canid, zapodid rodents, brachydont and mesodont heteromyids, and a diverse suite of artiodactyls (camelids, antilocaprids, and peccary). The Wye LF contains 20 taxa that are not found higher in the section. Large mammals that are present only in the Wye LF include the antilocaprid, camels, peccary, and the rhinoceros. Heteromyid species are diverse, but certain taxa (*Paratrogomys whistleri*, *Mookomys "altifluminus,"* *Proheteromys sulculus*) are restricted to Crowder Formation Unit 1. Zapodid rodents are present only in the Wye LF of Crowder Formation Unit 1.

The Squaw Peak LF (Table 3; latest He2) contains only one artiodactyl (a cervoid), mesodont and hypsodont heteromyids, and a single species of cricetid rodent. The cervoid (*Aletomeryx* sp.) only occurs in bed 17 (latest Hemingfordian correlative, He2) of Crowder Formation Unit 1. *Aletomeryx* is not found in the Cajon Valley Beds or in the Barstow Formation. Four taxa from the Squaw Peak LF are also known from the Hemingfordian age Wye LF. Two taxa make their first appearance in the Squaw Peak LF, and these persist into the Barstovian age Sulfur Spring LF (Table 2). The co-occurrence of Hemingfordian and Barstovian age taxa suggests that the Squaw Peak LF is transitional between earlier and later land mammal ages.

The Sulfur Spring LF (Table 4) contains two species of cricetids and the first occurrence of ochotonids from within the Crowder Formation. Also present are *Hypolagus* sp., *Archaeohippus mourningi*, and a large "*Merychippus*" sp. This local fauna contains the only leporids that are known from the Crowder Formation.

Locality CR 4-4, from a paleosol that is rich in carbonate kernels, is mapped as occurring near the base of Unit 4 of the Crowder Formation, but lithologically it appears to be at the top of Unit 3, beneath the brown silts of Unit 4 (Table 1). This locality (CR 4-4) produced nine taxa (Table 5), only one of which (*Perognathus furlongi*) is known from the lower stratigraphic horizons of the formation. Geomyoids and large cricetids are

Table 4 Barstovian local faunas, Crowder Formation beds 17 to 23, Cajon Valley, San Bernardino County, California.

	Squaw Peak Local Fauna	Sulfur Spring Local Fauna			
	Upper Unit 1 Barstovian	Lower Unit 2 Barstovian			
Taxa	Bed 17	Bed 19	Bed 20	Bed 22	Bed 23
Tamias sp.	•				
Mookomys "altifluminus"	•				
Perognathus furlongi	•				
Proheteromys sulculus	•				
Copemys tenuis	•				
Sinclairomeryx sp.	•				
Balantiomys crowderensis	–	•			
Miospermophilus cf. *M. wyomingensis*	•	•			
Russellagus sp.		•	•	•	
Hesperolagomys sp.		•	–	•	
Petauristodon sp. cf. *P. matthewsi*	•	•	–	–	•
Cupidinimus halli	•	–	–	–	•
Copemys tenuis	•	–	–	–	•
Copemys pagei					•
Archaeohippus mourningi	•	–	•	–	•
Hypolagus sp. (small)				•	
"*Merychippus*" sp. (large)					•

Table 5 Middle Hemphillian fauna, locality Crowder 4-4, Crowder Formation, Cajon Valley, San Bernardino County, California.

Mid-Hemphillian Taxa	Ba	Cl1	Cl2	Hh1	Hh2	Hh3	Hh4
Perognathus furlongi	—	—	—	—	•		
Cupidinimus lindsayi	—	—	—	—	•		
Copemys dentalis	—	—	—	—	•		
Copemys esmeraldensis		—	—	—	•		
Pliosaccomys magnus			—	—	•	—	
Parapliosaccomys oregonensis				—	•	—	
Parapliosaccomys sp. nov.				—	—		
Peromyscus pliocenicus				—	•	—	
Neotoma (*Paraneotoma*) sp.					•	—	—

present only in the assemblage from locality CR 4-4.

There are certain taxonomic consistencies throughout the Crowder Formation. Sciurids, *Perognathus furlongi* and other heteromyid rodents are present in all levels. Dipodomyinae and small cricetids (*Copemys* sp.) are present in the Squaw Peak LF, the Sulfur Spring LF, and the assemblage from locality CR 4-4.

All paleosol beds were sampled in equal volumes; however, the numbers of taxa in the samples vary throughout the section. For instance, 21 vertebrate taxa are found in beds 1 and 1U. The count decreases going up-section, to reach a low of only two taxa in beds 9 and 12, then the diversity increases to eight taxa in bed 15, then decreases to zero taxa in paleosols 16 and 18, whereas bed 17 produced seven taxa. Beds 19, 20, 22, and 23 (Table 4) each average four taxa, with no more than six taxa in bed 23. This discussion emphasizes the taxa that were found in the lower three of the five mappable units within the Crowder Formation.

Crowder Formation Unit 1

The Wye LF includes taxa from Unit 1, in beds 1 to 15; the Squaw Peak LF includes taxa from the upper part of Unit 1, in bed 17. The leptarctine carnivore *Leptarctus* cf. *Leptarctus ancipidens* is known from bed 1; *Miomustela* is known from beds 1, 2, 4, and 5; and *Aletomeryx* (*Sinclairomeryx*) *riparius* is known from bed 17. Immigrant taxa that define the Hemingfordian include *Leptarctus*, *Miomustela*, and *Aletomeryx* (Tedford et al., 2004). Tedford et al. (2004) noted that the early part of the Hemingfordian is characterized by the earliest appearance of *Cupidinimus* (which occurs in Crowder Formation bed 17) and includes the latest occurrence of *Menoceras* in midcontinent deposits. This suggests that beds 1 through 17 span a portion of the Hemingfordian (see Tables 2–4).

Petauristine flying squirrels (*Petauristodon matthewsi*) were recovered in Crowder Formation beds 1, 2, 5, and 15, and the cricetine rodent *Copemys* occurs in Crowder Formation bed 17. Large mammals found in Crowder Formation Unit 1 include *Parapliohippus* (*Parapliohippus carrizonensis*, Crowder Formation beds 1, 2, 4, 12, and 15), the small antilocaprid (cf. *Merycodus*, Crowder Formation bed 1), and the large camel *Aepycamelus* (Crowder Formation beds 1 and 3). The late Hemingfordian (He2 of Tedford et al., 2004) is defined by the earliest appearance of the immigrant petauristine flying squirrels (*Petauristodon* sp.) and the late Hemingfordian occurrence of the immigrant cricetine rodent genus *Copemys*.

The He2 interval is also characterized by the earliest appearance of *Parapliohippus* (*P. carrizonensis*), small antilocaprids (cf. *Merycodus*), and the large camel *Aepycamelus*. These taxonomic first occurrences and taxonomic characterizations are generally from the midcontinent of North America (Tedford et al., 2004). If they are also characteristic for the Northern Great Basin Province (see "Methods and Materials"), then the presence of *Petauristodon matthewsi*, *P. carrizonensis*, cf. *Merycodus*, and *Aepycamelus* in bed 1 and superjacent strata indicates that Crowder Formation beds 1 to 17 are late Hemingfordian in age (or He2, ~17.5–16.0 Ma; see Tables 3 and 4). The Wye and Squaw Peak local faunas therefore are of late Hemingfordian age.

Assuming that Crowder Formation Unit 1 (Wye and Squaw Peak local faunas) spans most of He2, the stratigraphy contains the following interesting taxonomic occurrences. The temporal range of the rhinoceros *Menoceras* is now extended into He2 in the Northern Great Basin Province. The zapodid rodents *Pleisiosminthus* (bed 15) and *Megasminthus* (bed 1) are unique Western North American occurrences. *Megasminthus* (Table 2; bed 1) has previously been recorded only from midcontinental Barstovian age deposits (Korth, 1994). *Copemys tenuis* occurs in bed 17 (Table 3; late He2, Squaw Peak LF) with *Aletomeryx* (*Sinclairomeryx*) *riparius*. The He2 occurrence of the genus *Copemys* is similar to the occurrence of the genus in the Barstow Formation (Lindsay, 1995); however, the species differ between these two localities.

Table 6 Summary of taxa in the Hemingfordian to Barstovian transition, Crowder Formation, Cajon Valley, San Bernardino County, California.

Taxa	Unit 1 Hemingfordian Beds 1–16	Upper Unit 1 Barstovian Bed 17	Unit 2 Barstovian Beds 18–23
Deroceras sp.	•		
Helminthoglypta graniticola	•		
cf. *Sceloporus* sp.	•		
Gerrhonotus sp.	•		
Erycinae gen. et sp. nov. undetermined	•		
Miomustela sp. nov.	•		
Leptarctus sp. cf. *L. ancipidens*	•		
cf. *Tomarctus* sp.	•		
Paradomnina relictus	•		
Petauristodon sp. (small)	•		
Plesiosminthus sp.	•		
Megasminthus sp. nov. near *M. gladiofex*	•		
Paratrogomys whistleri	•		
Hesperocamelus (*Aepycamelus*) sp.	•		
Procamelus sp.	•		
Michenia agatensis	•		
Miolabis tenuis	•		
cf. *Merycodus* sp.	•		
Cynorca sp?	•		
Menoceras sp.	•		
Parapliohippus carrizoensis	•		
Tapiridae	•		
Mookomys "*altifluminus*"	•	•	
Proheteromys sulculus	•	•	
Aletomeryx (*Sinclairomeryx*) *riparius*		•	
Tamias sp.	•	•	
Balantiomys crowderensis	•	–	•
Perognathus furlongi	•	•	•
Perognathus minutus	•	–	•
Petauristodon sp., cf. *P. matthewsi*	•	–	•
Protospermophilus sp.	•	–	•
Miospermophilus sp., cf. *M. wyomingensis*	•	–	•
Archaeohippus mourningi	•	–	•
Cupidinimus halli		•	•
Copemys tenuis		•	•
Copemys pagei			•
Russellagus sp.			•
Hesperolagomys sp.			•
Hypolagus sp.			•
Hypolagus sp. (small)			•
"*Merychippus*" sp. (large)			•

Copemys species (originally one of the genera defining the Barstovian; Tedford et al., 2004) occur in the Crowder Formation. *Copemys tenuis* is found in bed 17 (Table 3; He2), and *C. tenuis* and *Copemys pagei* occur together higher in the section (bed 23, early Barstovian of Ba1 of Tedford et al., 2004; see Tables 3 and 4 herein). In Barstow Formation stratigraphy, the first occurrence of *C. pagei* is in the late He section (following Tedford et al., 2004:table 6.2; i.e., below the Steepside Quarry level), and it co-occurs with *C. tenuis* almost 1.5 Ma later (>14.8 Ma, Lindsay, 1972; Woodburne, 1991b) at the Skyline Tuff horizon (Lindsay, 1972, 1991, 1995).

At this writing, the southwestern Northern Great Basin Province now has two late Hemingfordian occurrences (Barstow and Crowder formations) of the genus *Copemys*. It is significant that *Copemys pagei* is the He2 occurrence at Barstow (Lindsay, 1972, 1995) and that *Copemys tenuis* occurs in the He2 levels of the Crowder Formation. The genus *Copemys* is a North

Table 7 Rates of deposition for the Crowder Formation Units 1 to 5, Cajon Valley, San Bernardino County, California.

Thickness (m) (Total 860+ m)	Units (Weldon, 1985)	Span (Ma)	Rate
400	Unit 5	>6.0	555 m/Ma combined Units 4 and 5
100	Unit 4		
100	Unit 3	>7.1	20 m/Ma combined upper Unit 2 and Unit 3
50	Upper Unit 2	>14.8	
40	Lower Unit 2	16–14.8	33 m/Ma
170	Unit 1	17.2–16	142 m/Ma

American immigrant that was derived from *Democricetodon* of Asia (Lindsay, 1995). *Copemys tenuis* might derive from *C. pagei* (Lindsay, 1972). If so, the entry of this cricetid group into North America and its speciation into *C. pagei* and *C. tenuis* probably took place before 16.2 Ma (see Fig. 5; Lindsay, 1995).

Crowder Formation Unit 2

Paleosol beds 19 to 23 from the lower half of Crowder Formation Unit 2 produced vertebrate taxa composing the Sulfur Spring LF. In the Crowder Formation sequence, the ochotonids *Hesperolagomys* and *Russellagus* occur in Unit 2, beds 19 and 22 (Table 4). Remains of *Archaeohippus* from the Crowder Formation range through Unit 1 and 2 (in beds 1, 20, and 23; see Tables 2 and 4); they have not been morphometrically compared with the type specimen. A large species of "*Merychippus*" and two species of *Copemys* are also found in Unit 2 (in beds 19, 20, 22, and 23; see Table 4). Geologic mapping (Foster, 1980; Weldon, 1985) indicates conformable bedding attitudes, and recognizes no major unconformities within or between Unit 1 and Unit 2; hence, although deposition of these Crowder Formation units was by repeated fluvial pulses of arkosic sands separated by paleosols representing periods of stable soil development, there are no major temporal gaps between Units 1 and 2.

The Barstovian (Wood et al., 1941) is based on Northern Great Basin faunas from the Barstow Formation (see Tedford et al., 2004). First, last, and characteristic occurrences of Barstovian age taxa have been reviewed (Lindsay, 1995; Tedford et al., 2004), and the following discussion is based on their work, with emphasis on taxa that have been found in lower Crowder Formation Unit 2 (Foster, 1980; Weldon, 1985) from paleosol beds 19, 20, 22, and 23 (see Table 4).

Immigrants defining the beginning of the Barstovian and the early Barstovian, such as *Plithocyon* and *Zygolophodon* (Tedford et al., 2004) are not known from the Crowder Formation. Other taxa that have been used to characterize the early Barstovian (Ba1 of Tedford et al., 2004) are not useful temporal indicators in the Crowder Formation. For example, *Perognathus* spp. (*Perognathus furlongi* He, Ba, and Hh and *Perognathus minutus* He and Ba) have a longer range in Crowder, Barstow, and Sespe formation stratigraphic sections (Tables 4 and 6; Lindsay, 1991, 1995; Whistler, personal communication, 1999), and a review of rodents (Lindsay and Reynolds, 2008) indicates that *Balantiomys* (previously *Peridiomys* and formerly Barstovian) ranges through Crowder Formation Units 1 and 2 (He–Ba).

Tedford et al. (2004) presented taxa that define and characterize the late Barstovian, and they noted which occur in the Great Plains and Gulf Coast provinces. Of those that occur in the Crowder Formation sequence (*Hesperolagomys*, *Russellagus*, and *Megasminthus*), the latter two are geographically characteristic of the late Barstovian in the midcontinent Great Plains and Gulf Coast provinces. The ochotonids *Hesperolagomys* and *Russellagus* occur stratigraphically above bed 17 (He2) in Crowder Formation Unit 2 beds 19 and 22. Note also that *Megasminthus* sp., a form near but not identified as *Megasminthus gladiofex*, occurs in lowest Crowder Formation strata (late He Crowder Formation Unit 1 bed 1). Last occurrences in the late Barstovian, Ba2, include *Megasminthus* and *Archaeohippus* (Tedford et al., 2004). In Crowder Formation biostratigraphy, the presence of *Hesperolagomys*, *Russellagus*, *Archaeohippus*, a large "*Merychippus*," and two species of *Copemys* suggest that Unit 2 beds 19, 20, 22, and 23 (Table 4) fall within the Barstovian.

Crowder Formation Unit 3

Locality CR 4-4 is mapped as occurring near the base of Unit 4 but lithologically appears to sit at the top of Unit 3 beneath the brown silts of Unit 4 (Table 1). The CR 4-4 LF contains nine taxa (Table 5) including *Pliosaccomys*, *Parapliosaccomys* spp., *Paraneotoma*, *Peromyscus plioceni-cus*, *Copemys dentalis*, *Copemys esmeraldensis*, *Cupidinimus lindsayi*, and *Perognathus furlongi*. The beginning of the Hemphillian (Tedford et al., 2004) is defined in part by the first appearance of *Pliosaccomys*; *P. pliocenicus* is also found in the earliest Hemphillian deposits (Wilson, 1937; Korth, 1997). The immigrant *Paraneotoma* is

one taxon used to define the beginning of Hh3 and, in association with *Pliosaccomys* and the presence of two Crowder Formation species of *Parapliosaccomys*, suggests that the time of deposition of uppermost Crowder Formation Unit 3 was mid-Hemphillian NALMA (about 7 Ma; Table 5; Reynolds, 1999). In the CR 4-4 LF, *Paraneotoma sp.* seems to occur earlier than elsewhere in the southwestern Northern Great Basin Province. *Copemys* diversity is reportedly limited in the Hemphillian (Baskin, 1979; Czaplewski, 1990), but two late Barstovian/Clarendonian species, *C. dentalis* and *C. esmeraldensis* (Clark et al., 1964), persist into the Hemphillian at the CR 4-4 locality. The heteromyids *P. furlongi* and *C. lindsayi* are also found at this locality (Table 5), demonstrating their longevity from the Hemingfordian and Barstovian ages through the Hemphillian.

BIOSTRATIGRAPHIC SUMMARY

The He2 age of the Wye and Squaw Peak local faunas (Crowder Formation Unit 1) is supported by the presence of *Petauristodon* species in association with *Leptarctus*, *Miomustela*, *Menoceras*, and *Aletomeryx* (Tables 5 and 6). There is an early occurrence of the Zapodid rodent *Megasminthus* within the He2 Wye LF, and *Menoceras* may be considered a local provincial holdover from He1. In the Squaw Peak LF, the first occurrence of *Copemys* sp. heralds the end of the Hemphillian.

The Barstovian age of Crowder Formation Unit 2 is supported by the presence of the leporids *Hesperolagomys*, *Russellagus*, *Hypolagus*, the large "*Merychippus*," and two species of *Copemys* (*C. tenuis* and *C. pagei*).

The Hemphillian age of the upper part of Unit 3 of the Crowder Formation is supported by the presence of *Pliosaccomys* sp. and *Peromyscus pliocenicus*. The immigrant *Paraneotoma* supports the middle Hh age determination (Table 5). Small cricetids (*Copemys dentalis*, *Copemys esmeraldensis*) are considered to be holdovers/range extensions from the Clarendonian.

The Crowder Formation section provides a new look at early taxonomic occurrences in the He (*Copemys* and *Megasminthus*), in the Ba (*Hesperolagomys* and *Russellagus*), and in the Hh (*Paraneotoma*) that may reflect North American continental biogeographic differences (Barnosky, 1986; Lindsay, 1995; Tedford et al., 2004).

Regional Comparisons

The Crowder Formation's faunal sequence was deposited on the east side of the right-lateral San Andreas Fault. The only biostratigraphic sequence on the west side of that fault with late Hemingfordian to early Barstovian small mammals is in the Caliente Formation of the California Coast Ranges (James, 1963; Kelley and Lander, 1988; Tedford et al., 2004) and is located 100 miles (~160 km) to the northwest. At such other Mojave Desert localities as the Barstow Formation (see Lindsay, 1972, 1995; Woodburne et al., 1990; Woodburne, 1991b) and the Cajon Valley Beds (see Woodburne, 1991a:table 9), vertebrates are rare in the late Hemingfordian sedimentary sequence (Toomey Hills LF, Daggett Ridge LF, upper Cady Mountains LF, Alvord Mountains LF; see Reynolds, 1991b; Woodburne, 1991b) and rarely occur in a stratigraphic sequence.

In addition to the geographic range extensions of *Pleisiosminthus* and *Megasminthus* into the southwestern Northern Great Basin Province, new rodent taxa and their distribution through the Crowder Formation have been described (Lindsay and Reynolds, 2008). *Paratrogomys whistleri* is a new heteromyid rodent that was possibly derived from the Arikareean *Trogomys rupedimenthi* (see Reeder, 1960; Whistler, 1984; Korth, 1997). *Paratrogomys whistleri* is found in Crowder Formation Unit 1 (beds 1–15, He2; Table 6). *Balantiomys crowderensis* is a new peridiomyine heteromyid of the subfamily Mioheteromyinae (Lindsay and Reynolds, 2008) that is distributed through the Hemingfordian and Barstovian portions of Crowder Formation Units 1 and 2 (beds 1, 5, 19; see Table 7).

The geographic range extensions of rodents represented by the early occurrences (*Megasminthus* sp., *Perognathus* sp., *Cupidinimus halli*, *Copemys tenuis*) and late occurrence (*Menoceras* sp.) in Crowder Formation Unit 1 (Table 6) might represent local provinciality in the southwestern Northern Great Basin Province. Similarly, the ochotonids *Hesperolagomys* and *Russellagus* (Crowder Formation Unit 2) might occur earlier in this province than in the midcontinent Great Plains and Gulf Coast provinces (Tables 4 and 7; see Tedford et al., 2004:215).

In the Hemphillian fauna (CR 4-4 LF; Table 5), the association of gopheroids (*Pliosaccomys*, *Parapliosaccomys*) and small Clarendonian cricetids (*Copemys dentalis*, *Copemys esmeraldensis*) with large cricetids (*Peromyscus pliocenicus*), including an ancestral *Neotoma* (*Paraneotoma* sp.), suggests that the small cricetids are extensions into the mid-Hemphillian (Reynolds, 1999). The presence of *Perognathus furlongi* and *Cupidinimus lindsayi* supports recognition of their long temporal ranges (Table 5 and 7).

Comparison to the Geomagnetic Polarity Time Scale

Magnetostratigraphy in the Crowder Formation (Weldon, 1985:fig. 4) was related to the formation's biostratigraphy (Reynolds, 1985) on the

basis that the Crowder Formation depositional sequence was a series of cyclic fluvial pulses recognized in outcrop as thick arkosic units separated by multiple paleosols, with only one minor stratigraphic scour at the top of Unit 2. We evaluate previously assigned age designations (Weldon, 1985) by comparing Crowder Formation local faunas of specific land mammal ages and the magnetic polarity signature of the Crowder Formation unit that contains each local fauna (Weldon, 1985:fig. 5) with the geomagnetic polarity time scale (GPTS).

The transition from early to late Hemingfordian occurs in the interval between 17.5 and 17.0 Ma (Tedford et al., 2004). Crowder Formation Unit 1 contains the immigrant petauristine flying squirrel (*Petauristodon matthewsi*, beds 1, 2, 5, and 15) and, in the upper part of Unit 1 (bed 17), the cricetine rodent *Copemys*. This suggests that Crowder Formation Unit 1 is late Hemingfordian in age and that the occurrence of *Menoceras* in Crowder Formation bed 4 is a holdover from the early Hemingfordian. Therefore, deposition of Crowder Formation Unit 1 started approximately 17.5 to 17.0 Ma, and continued through 16 Ma. The taxonomic assemblage from bed 1 occurs in a long reversal above three short normal intervals and below a long normal event followed by three short normal events (Weldon, 1985:fig. 4). This sequence of reversals places beds 1 to 4 in the lower portion of the reversed section of Chron C5C (~17.1–17.3 Ma; Fig. 5). Crowder Formation Unit 1 beds 5 to 17, with taxa characteristic of He2, would then span a period between 17 and 16 Ma, the last half of Chron C5C. The end of He2 and Chron C5C at 16 Ma (Tedford et al., 2004) falls between Unit 1 bed 17 and Unit 2 bed 19.

The Barstovian is recognized by the presence of *Archaeohippus*, "*Merychippus*," two species of *Copemys*, and the ochotonids *Hesperolagomys* and *Russellagus* in Crowder Formation Unit 2 beds 19, 20, 22, and 23. Therefore, the sediments between beds 19 and 23 (Unit 2) are within the Barstovian (16+ Ma). The magnetic sequence in the lower half of Unit 2 (beds 19–23) consists of a long reversal followed by two normal events in the upper half of Unit 2 (Fig. 4), superposed by more strong normals in Unit 3. A similar sequence appears in Chron C5B (= Crowder Formation Unit 2), followed by Chron C5AD and C5AC (= Crowder Formation Unit 3) of the GPTS (Weldon, 1985; Woodburne, 2004b). This suggests that the reversed polarity signature of Crowder Formation Unit 2 (beds 19–23) ranges from approximately 16.0 to 15.2 Ma and that the normal sediments in the upper part of Unit 2 represent the transition from C5B into C5AD approximately 15.2 to 14.8 Ma. This implies that taxa in beds 19 to 23 represent Ba1 and that the ochotonids *Hesperolagomys* and *Russellagus* occur earlier in the Crowder Formation than in Ba2 deposits from midcontinent (see Tedford et al., 2004:215; =Ba2).

The GPTS (see Berggren et al., 1995; Woodburne and Swisher, 1995; Tedford et al., 2004) shows that the early Hemphillian contains many strong reversal events that are broken by normals (C3BR, C3B), which are followed in Hh3/Hh4 by a long reversal culminating in two strong normals (C3A). Locality CR 4-4 is at the base of a long reversed period that spans Unit 4 (Fig. 4), with two minor normals near its top. The overlying Unit 5 has strong reversed magnetozones low in the unit, and many strong normal magnetozones high in the unit. For the Hemphillian indicator taxa (*Pliosaccomys* and *Paraneotoma*) to be associated at approximately 7 Ma, the best match to the GPTS would be deposition within Chron C3Br, suggesting an age of 7.1 Ma (Fig. 5). If that is so, then the occurrence of *Paraneotoma* in the Crowder Formation is 1 million years earlier than it has elsewhere been recorded.

Rates of Deposition

We have calculated rates of deposition for the Crowder Formation on the basis of land mammal ages of specific units relative to the GPTS (Table 8). Deposition within Crowder Formation Units 1 to 3 slowed from a rate of 100 m/Ma in Unit 1 to less than 20 m/Ma at the top of Unit 3. Unit 4 consists of brown silts, suggesting deposition in a poorly drained basin. The following pulse (Unit 5) of arkosic deposition was at a rate above 400 m/Ma.

Paleosols formed at a much slower rate than intervening arkosic fluvial lenses. Paleosols are absent in the lower two thirds of Unit 1; increase in frequency in upper Unit 1, Unit 2, and Unit 3; and are poorly developed or absent in upper Unit 4 and Unit 5, thus supporting the rates of deposition that are described (see Table 8). Foster (1980) mapped a marker bed near the top of Unit 2, truncated along 10% of its length by Unit 3, suggesting an erosional unconformity. This is the only physical evidence for a major depositional and temporal gap in the Crowder Formation depositional sequence.

Biostratigraphic Comparisons

Crowder Formation Unit 1 compares in part to the Red and Rak divisions at Barstow and to the Cajon Valley Beds Units 1 and 2, having *Parapliohippus*, *Archaeohippus*, *Leptarctus*, and *Probeteromys sulculus* in common (Lindsay, 1995; Reynolds, 1991a; Woodburne 1991b) (see Fig. 3). The Crowder Formation lower Unit 2 fauna compares in part with the Green Hills Fauna at Barstow (Woodburne, 1991b) and the Cajon Valley Beds Units 5 and 6 (Reynolds, 1991a; Woodburne, 1991a) by having *Cupidinimus halli*, *Perognathus*

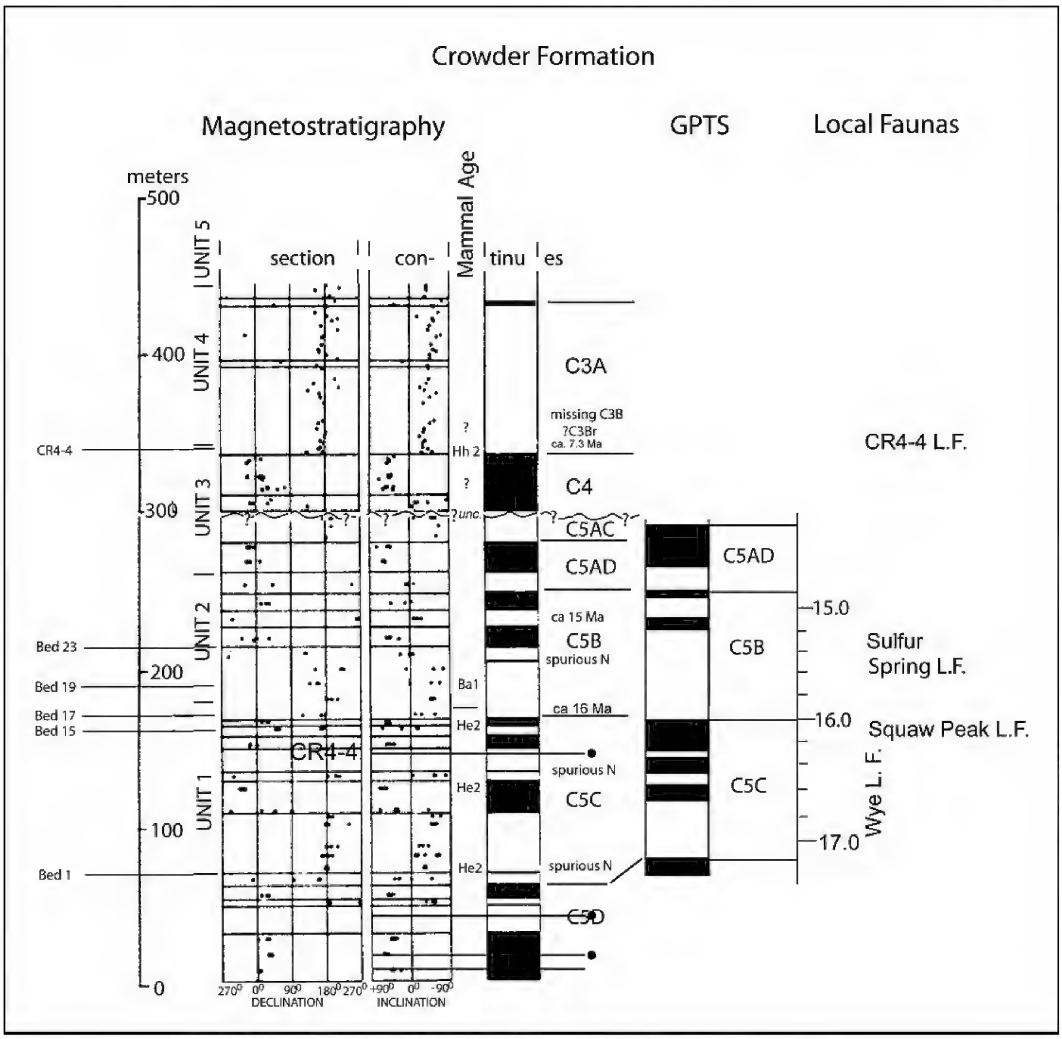

Figure 3 Comparison of Crowder Formation magnetostratigraphy (after Weldon, 1985) to the geomagnetic polarity time scale.

furlongi, *Copemys tenuis*, *Copemys pagei*, *Archaeohippus mourningi*, *Hypolagus* sp., and a large "*Merychippus*" in common.

The mid-Hemphillian portion of Crowder Formation upper Unit 3 might compare in part to the upper part of the Dove Spring Formation in Red Rock Canyon, Kern County, California (Whistler and Burbank, 1992), where *Copemys dentalis* occurs in sediments of early Hemphillian age. Hemphillian NALMA faunas are absent from the sequences at Barstow and in the Cajon Valley beds.

DISCUSSION

The age of the Crowder Formation has been constrained by interpreting land mammal ages from four local faunas recovered from exposures in the lower half of the formation. Several taxonomic range extensions may be the result of biogeographic differences between the North American provinces. The range of *Menoceras*, a late He1 indicator, overlaps with *Petauristodon* (Tables 2, 6, 7), a He2 indicator. *Megasminthus*, normally a Ba indicator, makes its first Crowder Formation appearance with *Menoceras* and other He taxa (Tables 1, 5, 7). In the Crowder Formation, *Copemys tenuis* appears earlier than *Copemys pagei* (Tables 3 and 7) in contrast to the section in the Mud Hills at Barstow. The ochotonids *Hesperolagomys* and *Russellagus* appear early in the early Ba of the Crowder Formation (Table 7), in contrast to midcontinent occurrences. *Neotoma* (*Paraneotoma*) makes an early appearance in the Hh with the early Hh geomyids, *Pliosaccomys* and *Parapliosaccomys*,

Table 8 Comparison of lithostratigraphic and biostratigraphic sections, Cajon Valley Beds, Crowder Formation and Barstow Formation, desert areas of Southern California.

Ma	GPTS	NALMA	Southwest Cajon Valley Beds	Crowder Fm.	Northeast Barstow Fm.
				Unconformity	
6		Hh3		Unit 5	
				Unit 4	
7.1	C3Br	Hh2	Unconformity	Upper Unit 3 Unconformity?	Unconformity
13	C5A	Ba2	Unit 6	Lower Unit 3	Upper Division
15		Ba2	Unit 5	Upper Unit 2	Second Division
15.5	C5Bn	Ba1	Unit 4	Lower Unit 2	Green Hills
			Limited Clastic Wedge	Upper Unit 1 (Bed 17)	
<16	C5Br				
>16	C5Cn	He2	Unit 3	Upper Unit 1 (Beds 1–15)	Rak Division
	C5Cr				Red Division
17.2	C5Cr	He2	Unit 2	Lower Unit 1	Owl
				(Beds 1–15)	Conglomerate
			Unit 1		

and the cricetids, *Copemys esmeraldensis* and *Copemys dentalis*, the latter two formerly considered to extend into the late Clarendonian and early Hh, respectively.

ENVIRONMENT OF DEPOSITION

The Wye and Squaw Peak local faunas (Crowder Formation Unit 1; Tables 5 and 6) contain flying squirrels (*Petauristodon*), rhinoceros (*Menoceras*), and cervoids (*Aletomeryx*). Associated mollusks and reptiles from this local fauna suggest a habitat that was stabilized by brush and trees and covered with leaf litter.

The Squaw Peak LF has reduced taxonomic diversity (Table 7) and contains low-, medium-, and high-crowned heteromyids, the cervoid, and the first occurrence of a small cricetid (*Copemys* sp). The reduced taxonomic diversity and abundant heteromyids might be explained by the increased rates of deposition (Table 8) representing an active fluvial environment with reduced woodland.

Crowder Formation Unit 2 fauna includes leporids (*Hesperolagomys*, *Russellagus*, *Hypolagus*), a large "*Merychippus*," and two species of *Copemys* (*C. tenuis* and *C. pagei*). The taxa suggest a mix of parkland and grassland.

Abundant geomyids and large and small cricetids of the Hemphillian CR 4-4 LF suggest habitat that is dominated by grassland, with scrub brush margins.

CONCLUSIONS

1. The Crowder Formation in the Cajon Valley area of San Bernardino County, Southern California, provides a stratigraphic sequence of early Miocene biostratigraphic changes on the southwestern margin of the Northern Great Basin Province. Crowder Formation Unit 1 is Hemingfordian, He2; Unit 2 is Barstovian; and the single locality in the uppermost part of Crowder Formation Unit 3 produces rodents of the mid-Hemphillian NALMA.
2. Faunal indicators of late Hemingfordian (Table 7) occur in Crowder Formation Unit 1, suggesting that deposition started approximately 17.5 to 17.0 Ma (Figs. 4 and 5; Tedford et al., 2004). Heteromyid species are diverse, but certain taxa (*Paratrogomys whistleri*, *Mookomys* "*altifluminus*," *Probeteromys sulculus*) are restricted to the Hemingfordian. Zapodid rodents are present only in the Wye LF.
3. Low in the section there is an interesting co-occurrence of *Menoceras*, *Petauristodon*, and *Parapliohippus*, suggesting that the rhinoceros is a provincial holdover. The end of He2 and Chron C5C at approximately 16 Ma would be between Crowder Formation Unit 1 bed 17 and Crowder Formation Unit 2 bed 19 (Fig. 5). The existing magnetic signature (Fig. 4; Weldon, 1985) for Crowder Formation Unit 1 beds 1 to 17 correlates with Chron C5C of the GPTS. Crowder Formation Unit 1 may span the period between 17.2 Ma and 16 Ma.
4. Barstovian NALMA taxa are recognized in Crowder Formation Unit 2 beds 19 to 23 (Table 7). The magnetic signature (Fig. 4; Weldon, 1985) is similar to Chron C5B. This suggests that the lower half of Crowder Formation Unit 2 (beds 19–23) ranges in age from approximately 16.0 to 15.2 Ma. The ochotonids *Hesperolagomys* and *Russellagus* apparently occur earlier in the Crowder

Formation than in midcontinent deposits (see Tedford et al., 2004:215).

5. The best comparison for mid-Hemphillian taxa from Crowder Formation locality CR 4-4 is with Chron C3Br (7.1 Ma; Table 8) of the GPTS. These comparisons suggest that previously undetected erosional and depositional unconformities might occur lower in Crowder Formation Unit 3 and that, not surprisingly, first occurrences of extra-local and immigrant taxa (such as *Paraneotoma;* see Reynolds, 1999) might differ in time between different North American provinces.
6. The Crowder Formation units have produced 40 mammalian taxa, including the new genera and species *Paratrogomys whistleri* (Lindsay and Reynolds, 2008), and *Balantiomys crowdernsis* (Lindsay and Reynolds, 2008). These deposits included reptiles and birds, as well as the remains of burrowing insects and millipedes. The recovery of over 9,000 vertebrate fossils from 20 paleosol horizons within the Crowder Formation stresses the importance of careful examination and collection from buried soil horizons.

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Fossil dogs (Carnivora, Canidae) from the Sespe and Vaqueros formations in Southern California, with comments on relationships of *Phlaocyon taylori*

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ABSTRACT. Six species within three subfamilies of Canidae were recovered from the Arikareean through Hemingfordian part of the undifferentiated Sespe/Vaqueros formations as a result of paleontologic resource mitigation activities during Orange County highway construction and landfill programs in Southern California. These can be identified as ?*Mesocyon* sp., *Cynarctoides whistleri* sp. nov., *Phlaocyon taylori*, *Desmocyon thomsoni*, *Metatomarctus canavus*, and *Leptocyon vulpinus*. Canids are generally rare in lower Miocene deposits of Southern California. Of the six species reported herein, only *Mesocyon* has previously been reported from California. In addition to California, the new species, *C. whistleri*, also occurs in Texas. *Cynarctoides whistleri* has a combination of primitive and advanced characters, suggestive of a transitional form that developed in isolation from the main area of evolution for *Cynarctoides* in the northern Great Plains. The new *Phlaocyon* material is only the third record of this species known, and it is the first record from outside of Florida. The new California specimen of *P. taylori*, with its nearly complete upper and lower dentitions, substantially improves our knowledge of, and greatly expands the distribution of this small, hypocarnivorous canid. The coyote- to fox-sized canids *Mesocyon*, *Desmocyon*, *Metatomarctus*, and *Leptocyon* are also known from the Great Plains, indicating wide distributions for these cursorial forms, whereas the two small, hypocarnivorous canids *Cynarctoides* and *Phlaocyon* seem to show regional differentiation, with distributions in Florida, Texas, and Southern California.

INTRODUCTION

Paleontological resource impact mitigation programs associated with the Foothill/Eastern Transportation Corridor toll roads and landfill projects in Orange County, Southern California, during the past 20 years have yielded a substantial collection of vertebrate fossils. More than 4,000 fossil vertebrate specimens, most of them isolated rodent teeth collected via screen washing and heavy-liquid separation techniques, were recovered from more than 100 fossil localities in exposures of the continental Sespe Formation and the undifferentiated Sespe and marine Vaqueros formations in the Santa Ana Mountains and San Joaquin Hills of the northern Peninsular Ranges Province (Whistler and Lander, 2003:fig. 11.1).

Six species belonging to three subfamilies of Canidae were recovered from reddish colored mudstones in terrestrial facies sediments in the Sespe and Vaqueros formations (Arikareean and Hemingfordian). These can be identified as ?*Mesocyon* sp.; *Cynarctoides whistleri* sp. nov.; *Phlaocyon taylori* Hayes, 2000; *Desmocyon thomsoni* (Matthew, 1907); *Metatomarctus canavus* (Simpson, 1932); and *Leptocyon vulpinus* (Matthew, 1907). These new materials fill a large gap in our knowledge of an ecologically diverse group of carnivorans from the late Cenozoic of North America.

Of the six canid taxa, only *Mesocyon* Scott, 1890, was previously known from the early Arikareean of California. The new species of *Cynarctoides* McGrew, 1938, shows regional differentiation of small, hypocarnivorous taxa in the southern United States. Three specimens of *P. taylori* from Orange County, with substantial upper and nearly complete lower dentitions, represent the best material for this species, which was previously known only by isolated teeth from Florida. The California specimens of *Phlaocyon* Matthew, 1899, are also the first records of the species outside of Florida, and they greatly expand the known distribution of this species.

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ABBREVIATIONS

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York USA
ETC	Eastern Transportation Corridor
FTC	Foothill Transportation Corridor
FTC/Oso	Oso segment of the Foothill Transportation Corridor
LACM	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA
LC	Ralph B. Clark Interpretive Center, Los Coyotes Regional Park, Buena Park, California USA
OCPC	Orange County Paleontological Collection, Santa Ana, California USA
PEAI	Paleo Environmental Associate, Inc., Altadena, California USA
RMW	RMW Paleo Associates, Inc., Mission Viejo, California USA
TMM-BEG	University of Texas Bureau of Economic Geology, now in the collection of Texas Memorial Museum, University of Texas, Austin, Texas USA
UF	Florida Museum of Natural History, University of Florida, Gainesville, Florida USA

GEOLOGY, AGE, AND ASSOCIATED FAUNA

Most of the canid-producing localities (e.g., LACM 6942, LC 166, LC 202, OCPC 2040) are in undifferentiated sediments belonging to the Sespe or Vaqueros formations, which range in age from the late Uintan to early Hemingfordian North American Land Mammal ages (Whistler and Lander, 2003). LACM 6942, which produced ?*Mesocyon* sp. and *P. taylori*, is in the eastern portion of the Frank R. Bowerman Landfill and covers an area of approximately 180 by 300 m. This locality consists of six fossil sites that were collected by personnel of RMW Paleo Associates, Inc., and later incorporated into a single LACM locality by Whistler and Lander (2003:fig. 11.3). The locality is recorded as being just above a local conglomerate in a composite stratigraphic section consisting of 190 m of variegated red sandstone/mudstone in the "Sespe" terrestrial lithofacies. The LACM locality description (entered by G.T. Takeuchi under the supervision of D.P. Whistler) states that LACM 6942 is "north of and apparently stratigraphically above LACM 7326," and that "these beds are steeply dipping to the north or there is a fault between localities." Locality LACM 7326, which produced *Sespia*, Stock, 1930, a typical early Arikareean oreodont, is near the bottom of the Bowerman Landfill section and below the conglomerate layer, which was used as a marker bed separating early and late Arikareean correlative strata (Whistler and Lander, 2003:figs. 11.2 and 11.3).

The biostratigraphic framework proposed by Whistler and Lander (2003:figs. 2 and 3) was based on a combination of field and faunal correlations, and stratigraphic controls might not be very precise because of the geologic complexities of the landfill property, the long sections often without distinct marker beds, and the limited time available for compiling stratigraphic data during grading. Given the complexity of faulting and the proximity of the six fossil sites included within LACM 6942, one cannot rule out the possibility that these sites might represent more than one stratigraphic horizon.

Of the two fossil canid sites included within LACM 6942, RMW SW 95-1309 was originally considered by D.P. Whistler (personal communication, 2003) to occur in early Arikareean correlative strata below the conglomerate. The other site, RMW TRM 043, was associated with localities LACM 6940 and 6944 that were considered to lie above the conglomerate. However, the *Phlaocyon* lower jaw described here is the only specimen obtained from RMW TRM 043, and lacking an associated fauna from this site, the possibility that TRM 043 might be of early Arikareean age cannot be ruled out.

The locality LC 202, which produced *P. taylori* and *L. vulpinus*, is at the bottom of the local stratigraphic section in the Oso Segment of the Foothill Transportation Corridor (FTC/Oso). This section, which does not contain the conglomerate, is correlated faunally with strata lying above the conglomerate elsewhere in Orange County (Whistler and Lander, 2003:figs. 11.3 and 11.4). Suspected to be a carnivore den, a sample from this site was screen-washed and yielded a small micromammal fauna. Besides the two canids (*P. taylori* and *L. vulpinus*) described here, Whistler and Lander (2003:table 11.2) listed the following micromammals from LC 202: *Herpetotherium* Cope, 1873; *Miospermophilus* Black, 1963; *Leidymys nematodon* (Cope, 1879); *Schizodontomys* Rensberger, 1973; and "*Nanotragulus ordinatus*? (Matthew, 1907)" (taxa in common from composite list for LC 202 + 205 in Whistler and Lander [2003] and from list in Lander and Whistler [1999]). Of these taxa, the hypertragulid *Nanotragulus* Lull, 1922, is significantly higher crowned than early Arikareean forms, and the heteromyine rodent *Schizodontomys* was listed in the late Arikareean and early Hemingfordian of Southern California (Whistler and Lander, 2003), but its range extends to the

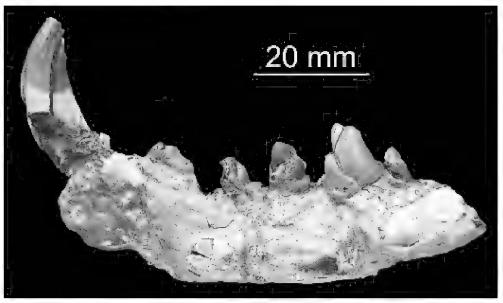

Figure 1 ?*Mesocyon* sp., LACM 148403, lateral view; from Bee Canyon Landfill locality, Orange County, California.

early Arikareean in the High Plains (Korth, 1994; Tedford et al., 2004). The other small mammals, however, have long temporal ranges that extend into early Arikareean time locally and/or regionally.

Locality LC 166, which produced *D. thomsoni* and *M. canavus*, is in the Santiago Canyon Landfill, a large, ongoing excavation that exposes interbedded dark red sandstone and green and yellow sandstones that are not differentiated between the Sespe or Vaqueros formations and are overlain by marine sandstones of the Topanga Formation. Fossils were recovered by PEAI and RMW personnel, and the resulting fossil assemblage, Santiago Canyon Landfill Local Fauna, is confined to the "Vaqueros" lithofacies (Whistler and Lander, 2003:fig. 11.3, table 11.2). Most of the localities in the Santiago Canyon Landfill produce the Upper OC S/V Fauna, which was postulated to be early Hemingfordian in age mostly on the basis of small mammals (Whistler and Lander, 2003:figs. 11.4 and 11.5).

As discussed herein, *Mesocyon* sp., *P. taylori*, and *L. vulpinus* suggest an early Arikareean age, as determined from their temporal relationships in our systematic studies (Wang, 1994; Wang et al., 1999; Tedford et al., in press), although remains from locality LC 202 possibly indicate a somewhat younger age. *Cynarctoides whistleri* sp. nov., *Desmocyon thomsoni* (Matthew, 1907), and *Metatomarctus canavus* (Simpson, 1932), on the other hand, are from the Hemingfordian part of the section.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Canidae Fischer de Waldheim, 1817

Subfamily Hesperocyoninae Martin, 1989

Mesocyon Scott, 1890

?*Mesocyon* sp.
Figure 1

REFERRED SPECIMEN. LACM 148403, left dentary fragment with broken c–m1, Bee Canyon Landfill locality (= Lower Bowerman Landfill locality of Whistler and Lander [2003] but different from their "Bee Canyon" locality), LACM locality 6942, site RMW SW 95-1309, at the end of Sand Canyon Road, north of the City of Irvine, Orange County, California (see further comments in "Geology, Age, and Associated Fauna" section above).

COMMENTS. LACM 148403 is severely crushed and distorted, and most of the teeth suffered considerable damage. Thus, it is not possible to observe many of the morphological features with certainty. The present taxonomic determination is therefore more of an exercise of weighing possibilities rather than a positive identification.

Relatively robust premolars with well-developed posterior accessory cusps and short m1 on LACM 148403 make this specimen unlikely to be a member of the Caninae. It is more difficult, however, to determine whether it belongs to the Hesperocyoninae or Borophaginae. With the exception of two highly derived species of *Phlaocyon* (see Wang et al., 1999), the majority of the late Arikareean and Hemingfordian borophagines are smaller than LACM 148403. That leaves the Hesperocyoninae as a more likely candidate. Within the Hesperocyoninae, *Mesocyon* comes closest to matching the overall morphology of this specimen, and the presence of a metaconid on the m1 rules out *Enhydrocyon* Cope, 1879b, and *Paraenhydrocyon* Wang, 1994.

Mesocyon has previously been reported from Arikareean age deposits of Southern California. Stock (1933) described *Mesocyon baileyi* from the Kew Quarry in the Sespe Formation (early Arikareean), a species that was synonymized with *Mesocyon brachyops* by Wang (1994). Walsh and Deméré (1991) reported *Mesocyon* from the Otay Formation (early Arikareean), which was identified more precisely as *Mesocyon coryphaeus* by Wang (1994). The specimen from Orange County is larger and more robust than the Kew Quarry form, and it is more consistent with the size of *M. coryphaeus*.

Subfamily Borophaginae Simpson, 1945

Tribe Phlaocyonini Wang, Tedford, and Taylor, 1999

Cynarctoides McGrew, 1938

Cynarctoides whistleri new species
Figure 2; Table 1

Cynarctoides gawnae Wang, Tedford, Taylor, 1999. Whistler and Lander, 2003:table 11.1.

Cynarctoides acridens (Barbour and Cook, 1914). Wang et al., 1999:62 (for TMM-BEG 40067-180 only).

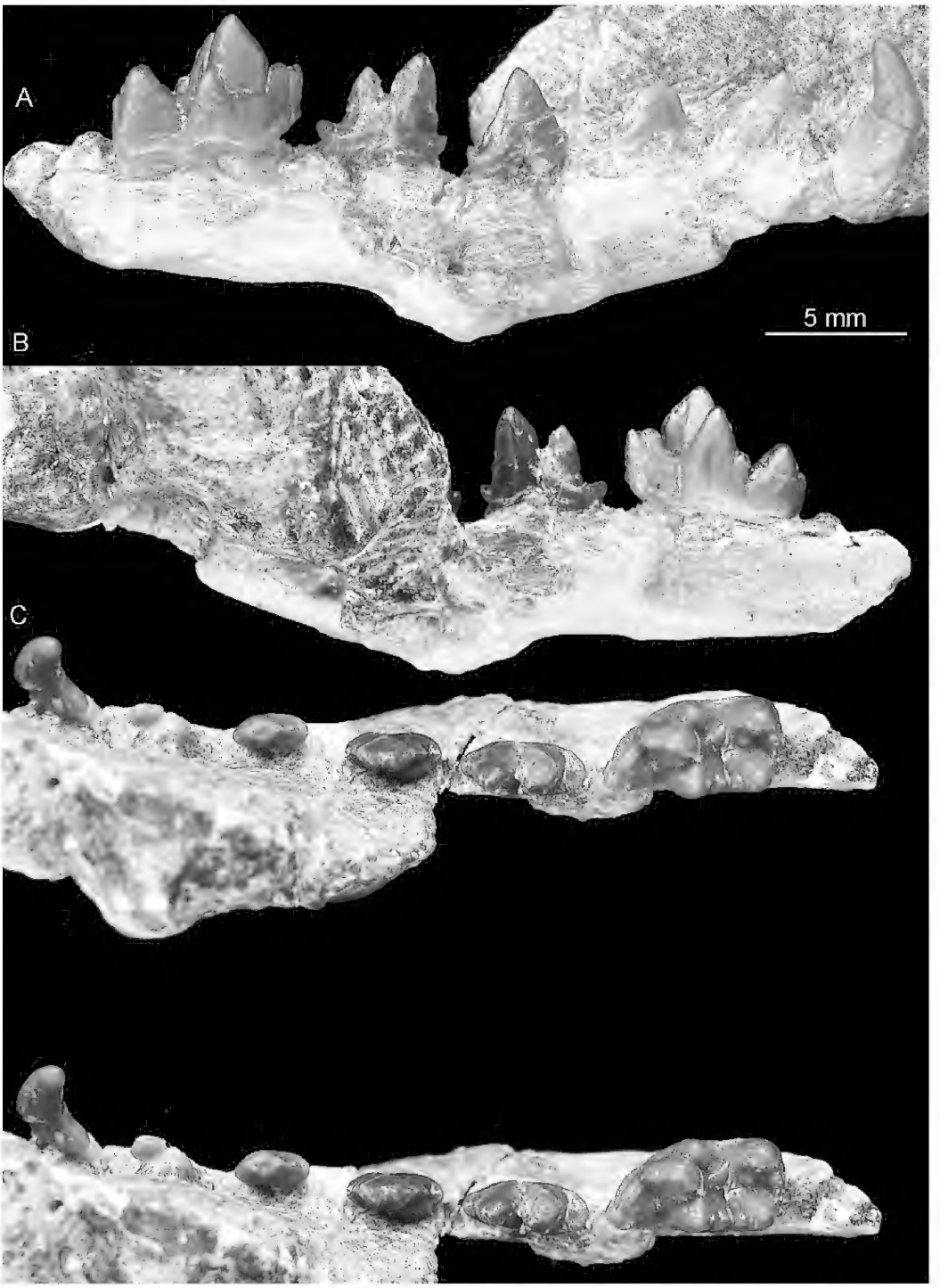

Figure 2 *Cynarctoides whistleri* sp. nov., OCPC 21796, holotype: **A,** labial; **B,** lingual; **C,** stereophotos of occlusal views.

Table 1 Dental measurements (mean, mm) of selected species of *Cynarctoides*; summary statistics adopted from Wang et al. (1999:appendix III).

	C. whistleri OCPC 21796	*C. luskensis*	*C. gawnae*	*C. acridens*	*C. emryi*
p1 length	1.53	—	2.30	2.23	—
p2 length	2.84	3.42	3.80	4.38	—
p3 length	3.57	4.14	4.60	5.05	4.73
p4 length	4.46	5.02	5.00	5.62	5.15
p4 width	1.88	2.29	1.95	2.47	2.60
m1 length	6.60	7.10	8.00	8.46	7.62
m1 Trigonid width	3.32	3.08	2.73	3.25	3.38
m1 Talonid width	3.40	3.43	3.27	3.84	4.00

HOLOTYPE. OCPC 21796, right horizontal ramal fragment with c–m1, field number GC.96.81.52, collected by Gino Calvano of Paleo Environmental Associates on 4 March 1996.

TYPE LOCALITY. OCPC locality 2040, Sec. 23, T4S, R8W, Windy Ridge, Orange County, California. OCPC 2040 is in an interbedded terrestrial and marine, maroon, silty sandstone in the undifferentiated sediments of Sespe or Vaqueros formations in the upper part of the Eastern Transportation Corridor (ETC) Windy Ridge section (Whistler and Lander, 2003:fig. 11.3). The locality is from the ETC Upper Windy Ridge Local Fauna, which belongs to the Upper OC S/V Fauna (Whistler and Lander, 2003: table 11.1, fig. 11.5), early Hemingfordian.

REFERRED SPECIMEN. TMM-BEG 40067-180 (cast AMNH 99659), isolated left m1, from Hidalgo Bluff, Texas A&M Museum locality 47, 5.5 miles (~8.9 km) northwest of Washington on the north side of the Brazos River, Washington County, Texas (Hesse, 1943:166–167). This specimen belongs to the Garvin Gully Fauna in the lower Oakville Formation, and it is middle Hemingfordian in age.

DIAGNOSIS OF SPECIES. *Cynarctoides whistleri* is more derived than primitive *Cynarctoides* species, such as *Cynarctoides lemur* (Cope, 1879a), *Cynarctoides roii* (Macdonald, 1963), and *Cynarctoide harlowi* (Loomis, 1932), in its transversely narrow premolars and high-crowned, cuspidate m1 talonid cusps. Compared with the slightly more derived species of *Cynarctoides luskensis* Wang, Tedford, and Taylor, 1999, and *C. gawnae*, it is also derived in its well-developed protostylid; tall-crowned m1 entoconid and hypoconid, which are of equal height; stronger crista obliqua; and presence of a narrow labial cingulum on m1 trigonid, all of which are characters that become more derived in *C. acridens* (Barbour and Cook, 1914) and *Cynarctoides emryi* Wang, Tedford, and Taylor, 1999. *Cynarctoides whistleri* differs from *C. acridens* and *C. emryi* in its primitive characters, such as m1 entoconid not exceeding hypoconid in height, protostylid and metastylid less well differentiated from the protoconid and metaconid, and less well developed crista obliqua. *Cynarctoides whistleri* has the following autapomorphies: short jaw; short and tall-crowned p2–3 without anterior and posterior accessory cusps, p4 with a very distinct posterior accessory cusp, m1 short and wide, and short m1 trigonid with an obliquely oriented paraconid blade.

ETYMOLOGY. The patronym honors David P. Whistler, curator emeritus of Vertebrate Paleontology at the Natural History Museum of Los Angeles County, for his careful documentation of Southern California vertebrate fossil records and dedicated service during his career in the museum.

DESCRIPTION. OCPC 21796 is a poorly preserved lower jaw from a young adult with fully erupted cheek teeth showing no wear. The horizontal ramus is fragmented into multiple pieces, and much of its ventral border, except a short segment below the p2, is missing. The anterior segment permits a sense of the depth of the dentary (4.5 mm). The horizontal ramus is slender, that is, dorsoventrally shallow and transversely thin, as is characteristic of *Cynarctoides*. The mental foramen is difficult to discern. The dentary posterior to the m1 is mostly missing, and only a partial alveolus for the anterior root of the m2 is present.

The lower canine is slender and recumbent. There is a lingual ridge on the anteromedial face of the tooth, and immediately posterior to it is a shallow groove. An indistinct ridge extends along much of the posterior side of the lower canine. The p1 is single-rooted. Its crown around the apex is preserved, but the basal part is damaged. The p2–4 are double-rooted and lack a cingulum on both lingual and labial sides. The p2 consists of a main cusp and a tiny posterior cingular cusp. The top part of the p2 main cusp is broken. The p3 is well preserved, and it is very high crowned. Besides its large main cusp, a tiny posterior accessory cusp is present, and there is a slight swelling on the anterior border on the p4. The p4 has both an anterior and a posterior cingular cusp, which are of similar sizes and larger than

those on the p3. A prominent posterior accessory cusp projects dorsal half way along the posterior ridge of the p4. The accessory cusp is distinct, high crowned, and of the same height as the m1 paraconid. The p4 main cusp has a slightly procumbent orientation, although part of this might be the result of a slight anterior shift of the main cusps because of postmortem distortion. As a result, the main cusp is slightly procumbent.

The m1 is short, mainly because of its lingually bent paraconid, in contrast to a more longitudinally oriented paraconid in most species of *Cynarctoides*. The paraconid is approximately half as tall as the protoconid, and it is also significantly lower than the metaconid. The protoconid is the tallest cusp of the tooth. A prominent protostylid is developed on the base of the posterolabial face of the protoconid. Behind the protostylid is a short labial cingulum between the protostylid and hypoconid. The apex of the protostylid is isolated from the main body of the protoconid. The metaconid is also high crowned, and it falls between the protoconid and paraconid in height. At its posterior base is a tiny metastylid immediately in front of a notch between the metaconid and entoconid. The talonid is wide. Both the hypoconid and entoconid have piercing, high-crowned tips and surround a deep talonid basin in the middle. The crown height of the two talonid cusps is about equal. The high, piercing talonid cusps result in deep notches anterior to the cusps, that is, between the metaconid and entoconid and between the protoconid and hypoconid. A small, but distinct, crista obliqua is oriented diagonally and intersects the posterior face of the trigonid just labial to the protoconid–metaconid notch. A small ridge is present posterior to the hypoconid and entoconid along the posterior rim of the talonid.

COMPARISONS AND DISCUSSION. Seven species of *Cynarctoides* were recognized in a revision of the borophagine canids by Wang et al. (1999): *C. lemur*, *C. roii*, *C. harlowi*, *C. luskensis*, *C. gawnae*, *C. acridens*, and *C. emryi*. In recognizing the new species from Southern California, we follow the phylogenetic framework developed by Wang et al. (1999). Within that framework, *C. whistleri* is at a stage of evolution between *C. gawnae* and *C. acridens* in terms of crown heights of m1 hypoconid, entoconid, and protostylid but is much smaller than late Arikareean and early Hemingfordian species of *Cynarctoides* (Table 1). Furthermore, the lower carnassial is much shorter than those of other contemporaneous species because of a more lingually bent paraconid blade, and it is also transversely wider. This short paraconid blade seems to suggest a more basal position for the California species, in contrast to the more derived cusp morphology on the m1. Associated with the short m1 is a short dentary and short premolars, a character that is absent among species from the Great Plains. The absence of upper teeth, however, prevents us from further analysis of the phylogenetic position of *C. whistleri*. Nevertheless, this combination of primitive and derived dental morphology for *C. whistleri* might suggest a geographic isolation of a southern lineage of *Cynarctoides*.

In further support of the possibility of geographic differentiation, we have identified a single m1 of early Hemingfordian age from Texas as belonging to *C. whistleri*. An isolated left m1 (TMM-BEG 40067-180, cast AMNH 99659) from the Oakville Formation of Washington County, Texas, was tentatively referred to *C. acridens* by Wang et al. (1999), but with a length of 6.6 mm, this specimen is at the lower end of the size range of the hypodigm of *C. acridens* (Wang et al., 1999:appendix III, table 1). We previously referred this m1 to *C. acridens* because of the stage of development of its protostylid, but it is now more logical to refer it to *C. whistleri*, following the discovery of the Southern California form.

Species of *Cynarctoides* have a long geologic time span of approximately 15 million years from early Arikareean to early Barstovian and, with the exception of *C. lemur* from the John Day Formation of Oregon and *C. acridens* from the Barstow Formation of Southern California, they are generally not found in the western coastal states. Despite the long chronologic range for the genus *Cynarctoides*, it displays its maximum diversity only in the late Arikareean and early Hemingfordian. *Cynarctoides whistleri*, the first reported occurrence of the genus in Hemingfordian strata of California, offers an opportunity to study the transitional morphology within the *Cynarctoides* lineage and permits a study of regional differentiation in the southern United States.

Cynarctoides is a highly unusual canid that demonstrates one of the few developments of secondary herbivory by carnivorans. The terminal species, *C. emryi*, developed modestly selenodont upper and lower molars, similar to those in primitive artiodactyls, that are unique among North American carnivorans. A rare parallel is seen among the Miocene lophocyonine viverrids of Europe (Fejfar and Schmidt-Kittler, 1984, 1987; Koufos et al., 1994). The less derived species of *Cynarctoides* developed tendencies toward ever more piercing cusp morphology that parallel dental features of insectivores. *Cynarctoides whistleri* appears to be a transitional species between the primitive forms (such as *C. lemur*, *C. luskensis*, *C. gawnae*) and the more derived species (*C. acridens* and *C. emryi*). In a clade of hypocarnivorous canids, it is perhaps not surprising to find this additional diversity in a more coastal (and possibly wooded) habitat in Southern California.

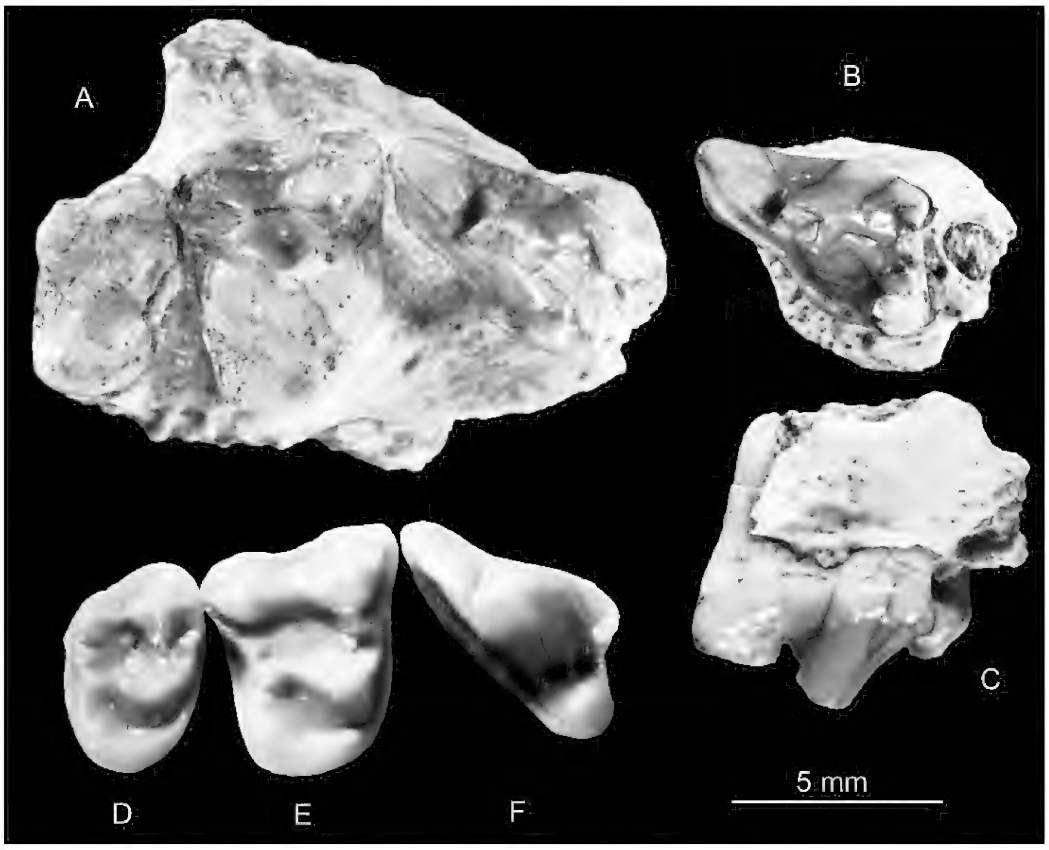

Figure 3 Upper teeth of *Phlaocyon taylori* Hayes, 2000, from California and Florida: **A,** right P4–M2, LC 9114; **B,** left P4 (reversed), LC 9112; **C,** lateral view of LC 9112; **D,** right M2, UF 163522; **E,** right M1, UF 163521; **F,** right P4, UF 163534. D, E, and F are photographs of polyester casts.

Phlaocyon Matthew, 1899

Phlaocyon taylori Hayes, 2000
Figures 3 and 4; Table 2

Phlaocyon spp. Whistler and Lander, 2003:table 11.2.

HOLOTYPE. UF 163524, an isolated left m1, Brooksville 2 Local Fauna, Hernando County, Florida (Hayes, 2000).

REFERRED SPECIMENS. LACM 148401, complete left horizontal ramus with c–m3, Bee Canyon Landfill locality (= Bowerman Landfill locality of Whistler and Lander [2003] but different from their "Bee Canyon" locality), LACM locality 6942, site RMW TRM 043, at the end of Sand Canyon Road, north of the City of Irvine, Orange County, California; LC 9112, left maxillary fragment with P4 and posterior root of P3, FTC/Oso locality, LC locality 202 (LC fossil site number GC 9781-167), Orange County, California; and LC 9114, maxillary fragment with right P4–M1, FTC/Oso locality, LC locality 202 (see further comments in "Geology, Age, and Associated Fauna" section above). See Hayes (2000) for additional referred specimens from Florida, except UF 163741, which is presently excluded from the hypodigm.

EMENDED DIAGNOSIS OF SPECIES. Well-developed P4 anterior cingulum, large protocone on P4, lingual cingulum enlarged to form precursor of hypocone; large upper molars relative to P4, transversely short M1–2, accessory cuspule of metaconules in M1–2; horizontal ramus slender; protostylid variably present on m1–2.

DESCRIPTION. The palate fragments are too poorly preserved to determine much of their morphology. The P4 is represented by two specimens (LC 9112 and LC 9114). These two teeth are nearly identical in size and shape (Table 2). The P4 in LC 9112 is better preserved and suffers from less wear. The overall proportions of the P4 are short and broad, which is characteristic of all *Phlaocyon*. There is a broad labial cingulum throughout the length of the

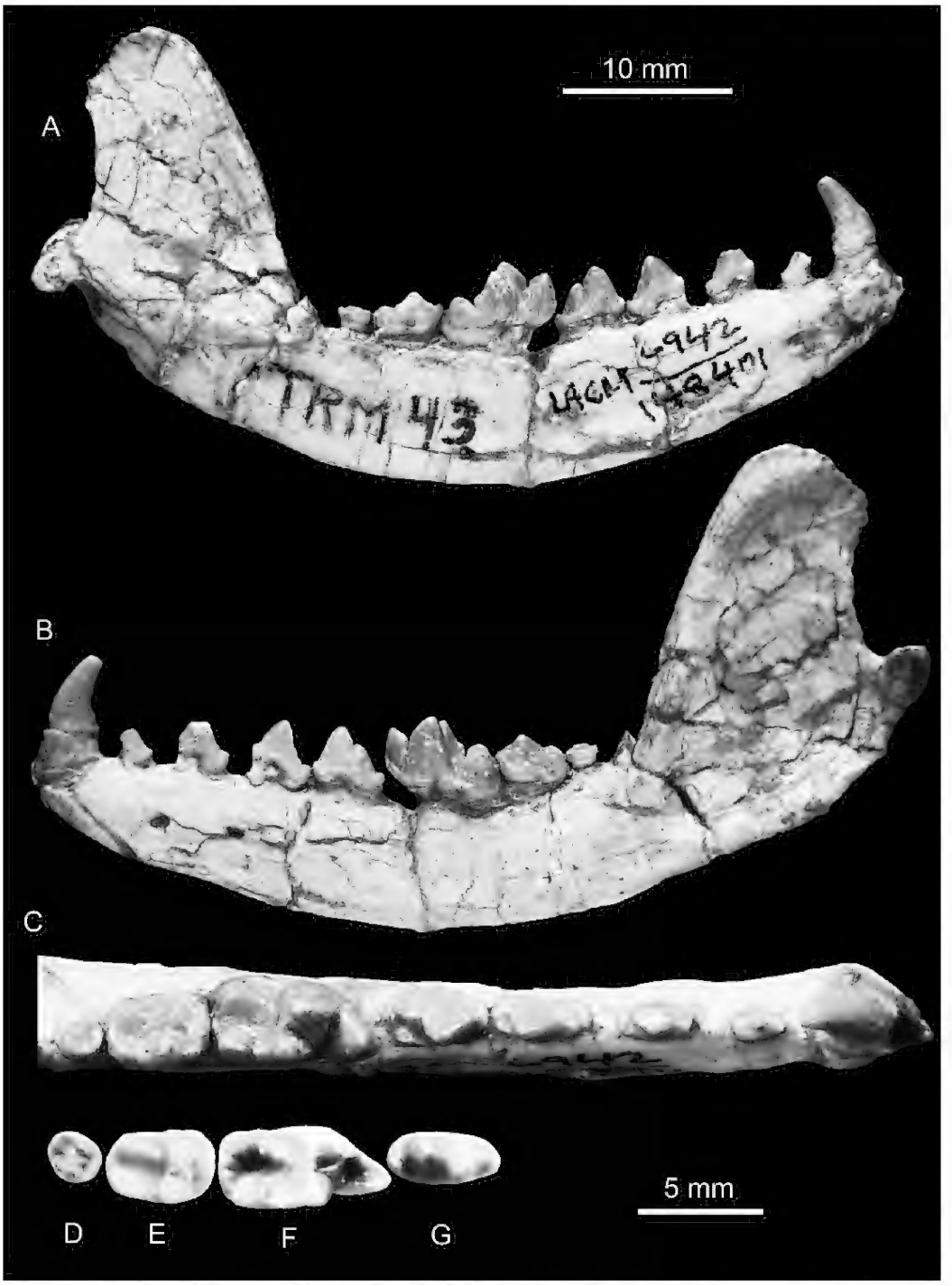

Figure 4 Lower jaw and teeth of *Phlaocyon taylori* Hayes, 2000, from California and Florida: **A–B,** left jaw, LACM 148401: **A,** medial view; **B,** lateral view; **C,** occlusal view of left lower teeth, LACM 148401; **D,** left m3, UF 163716; **E,** right m2 (reversed), UF 163511; **F,** left m1, UF 163524, holotype; **G,** right p4 (reversed), UF 163720. Upper scale is for A and B, and lower scale is for C–G.

Table 2 Dental measurements (mm) of *Phlaocyon taylori* Hayes, 2000, and *P. achoros* (Frailey, 1979) (those for *P. achoros* are from Wang et al. [1999]).

	Phlaocyon taylori				*Phlaocyon achoros*
	Southern California			Florida	Florida
	LACM 148401	LC 9114	LC 9112	Mean (n = 2–4)	Mean (n = 1–3)
P4 length		5.6	5.6	6.36	6.95
P4 width		3.5	3.6	3.55	4.25
M1 length		4.9		5.13	6.50
M1 width		6.4		6.25	7.60
M2 length		3.6		3.77	3.93
m2 width		5.4		5.17	5.50
p1 length	2.0				
p2 length	3.1				
p3 length	3.8				3.70
p4 length	4.2			4.95	5.10
p4 width	2.2			2.45	2.60
m1 length	6.4			6.73	8.50
m1 Trigonid width	3.1			2.83	3.10
m1 Talonid width	3.5			3.23	3.87
m2 length	3.9			4.77	5.15
m2 width	3.2			3.23	3.45

tooth (more so in LC 9112 than in LC 9114), although its lower boundary on the labial surfaces of the paracone and metastyle is not very distinct. The lingual cingulum is also well developed. The anterior part of the tooth is swollen to such an extent that it fills up the space posterior to the protocone. This swelling is too worn on both specimens to permit recognition of a hypocone, although a wear facet (created by occlusion with the lower carnassial blade) indicates the possible existence of such a cusp. The anterior cingulum at the base of the paracone is slightly elevated, suggesting a rudimentary parastyle. The P4 protocone is very large, conical, and anterior to the anterior border of the paracone. There is no cingulum surrounding the protocone.

The upper molars represented by LC 9114 are extremely worn. The M1 has a quadrate outline—anteroposteriorly long and transversely short—contrasting with the more transversely elongated outlines occurring in basal borophagines. A narrow labial cingulum and a much reduced parastyle are in contrast with those of the hesperocyonines. The paracone and metacone are nearly equal in size and positioned rather labially because of the narrow labial cingulum. Heavy wear in the lingual cusps prevents observation of the cusp patterns. The internal cingulum narrows anterolingual to the protocone. The M2 is similarly transversely short. Its paracone is surrounded by a labial cingulum, but the metacone is not. The paracone is larger than the metacone. The internal cingulum surrounds the protocone. As on the M1, cusps on the lingual half of the M2 are worn flat.

The dentary is known from a nearly complete left horizontal ramus (LACM 148301), which is extensively fractured but otherwise suffers little distortion. The horizontal ramus is shallow, with a depth of 7.5 mm below the m1. It has a nearly uniform depth through much of its length and tapers slightly anterior to the p3. There are two mental foramina: one between p1 and p2 and another between p2 and p3. The coronoid process of the dentary is rather erect, with a straight anterior border and a rounded dorsal border. The masseteric fossa is well delineated anteriorly and ventrally. The mandibular condyle is positioned on a plane dorsal to the occlusal surface of lower cheek teeth. The angular process is broken. The mandibular symphysis is long, reaching as far posteriorly as the middle of the p2.

The lower teeth are little worn, with only the tip of the lower canine showing signs of slight wear, and the other cheek teeth unworn. No incisor is preserved. The lower canine is recumbent, and it has an oval cross section throughout its length. There is no anterior or posterior ridge, and the enamel surface is free of wrinkles or ornamentation. There is no lingual cingulum, although a slight swelling is present in its place. The p1 is single-rooted and single-cusped. It is slightly procumbent with a much longer posterior ridge than the anterior ridge. There is no sign of an anterior or posterior cingular or accessory cusp. The p2 is double-rooted. Its main cusp is broken at the apex. As in the p1, the posterior ridge on the main cusp is considerably longer than the anterior ridge. In contrast to the p1, however, there is a slight swelling at the anterior base of the main cusp, although this swelling is not yet a

cusp. There is no posterior cingular cusp, but there is a slight suggestion of a talon at the posterior end of the tooth. The p3 is also single-cusped. Its anterior base is swollen a little more than that on the p2, but it is not a cusp. A longer posterior talon (shelf) is present. Along the apical portion of the posterior ridge there is a vague notch in contrast to a distinct notch on the p4. The p4 has a well-developed posterior accessory cusp delineated by the aforementioned notch. This accessory cusp is rather tall, exceeding half the height of the main cusp, and it is positioned labially off center in occlusal view. The accessory cusp is also swollen somewhat more toward the labial side. A tiny anterior cingular cusp is present on p4. The posterior cingulum is well developed, and it is elevated slightly at its posterior end to indicate a tiny posterior cingular cusp. The anterior and posterior cingula are not continuous around the main body of the tooth.

The m1 is relatively short and wide. The trigonid is short because of its lingually bent shearing blade. The protoconid is the largest and tallest cusp in the trigonid. The paraconid bends sharply lingually from the protoconid blade, such that the apex of the paraconid is set near the lingual border of the trigonid. The metaconid is set slightly posterior to the protoconid. It is strongly developed and taller than the paraconid. A small metastylid is present at the base of the posterior ridge of the metaconid, but there is no protostylid. The talonid is basined, surrounded by a larger and lower hypoconid and a smaller and taller entoconid. The hypoconid is ridgelike, and it extends anteriorly to the posterior base of the trigonid. The posterior ridge of the hypoconid bends lingually and tapers toward the talonid basin. The entoconid is significantly taller than the hypoconid. Its anterior ridge is cut off by a sharp notch between the entoconid and metastylid. There is a tiny hypoconulid at the posterior end of the talonid, which is not tall enough to surround the talonid basin, that is, the basin is open posteriorly. There is no lingual cingulum surrounding either the trigonid or the talonid. An indistinct labial cingulum is present around the carnassial notch, and there is also a short cingulum between the trigonid and talonid.

The m2 is relatively large. The paraconid is absent and its position is indicated by a low shelf anterior to the protoconid. The metaconid is much larger and taller than the protoconid, but, unlike the m1, it does not have a metastylid. The apex of the metaconid is slightly posterior to that of the protoconid. The protoconid is centrally located, and posterolateral to it is a small protostylid at the base of the protoconid. The bicuspid talonid is formed by a large hypoconid and a small entoconid; the two cusps enclose a small basin. The hypoconid is similar to that on m1, and it is ridgelike and oriented anteroposteriorly. The entoconid is of the same height as the hypoconid, and it is positioned on the posterolingual corner of the tooth. As on the m1, there is a notch between the metaconid and entoconid. There is no lingual cingulum. A labial cingulum is present at the anterolabial corner of the tooth.

The m3 is a small, circular tooth with very low cusps. There are two indistinct cusps on both lingual and labial borders of the tooth.

COMPARISONS. An exceptionally small, reduced M1 parastyle, and basined talonid on the m1 indicate that this specimen (LACM 148401) does not belong to the subfamily Hesperocyoninae (see Wang, 1994). Although its shallow horizontal ramus might suggest relationships to early members of the subfamily Caninae, such as *Leptocyon* Matthew, 1918, the teeth show no characteristics of that subfamily. *Phlaocyon taylori* lacks the narrow and elongated premolars and a long, longitudinally oriented, shearing blade on the upper and lower carnassials—derived characters that are typically present in members of the Caninae (Tedford et al., 1995).

Within the subfamily Borophaginae, early forms are dominated by the hypocarnivorous tribe Phlaocyonini, which is defined by a single derived character: a protostylid on the lower molars (Wang et al., 1999). This feature is weakly present in LACM 148401. Of the two genera within the Phlaocyonini, basal *Cynarctoides* (such as *C. lemur*) further shares with the present taxon a slender horizontal ramus. However, the California form resembles species within the genus *Phlaocyon*, as indicated by a number of shared derived characters: short and stout premolars, reduced P4 relative to size of upper molars, large and anteriorly located protocone of P4, enlarged lingual cingulum of P4 that tends to form a hypocone, quadrate (transversely short) upper molars, and a wide m1 talonid.

Hayes (2000) recently described *P. taylori* on the basis of 37 isolated teeth from the Brooksville 2 Local Fauna in central Florida and two referred teeth (a canine and a p4) from the Cow House Slough Local Fauna in southern Florida. The California form falls within the proportions and size range of *P. taylori* (Fig. 5), which is the smallest known species of *Phlaocyon*. Although the California material generally compares favorably with the Florida counterparts, there are a few minor differences. In general, the Florida topotypic specimens tend to have a less expanded lingual cingulum on P4, a better developed protostylid (especially on the m1), and a more distinct metastylid (entoconulid) on m1 (Figs. 3 and 4). These differences are likely the result of intraspecific variation over a wide geographic area and differences in stage of evolution between samples of different ages (see further comments below). The associated lower teeth of LACM 148401 also permit recognition of a misidentified

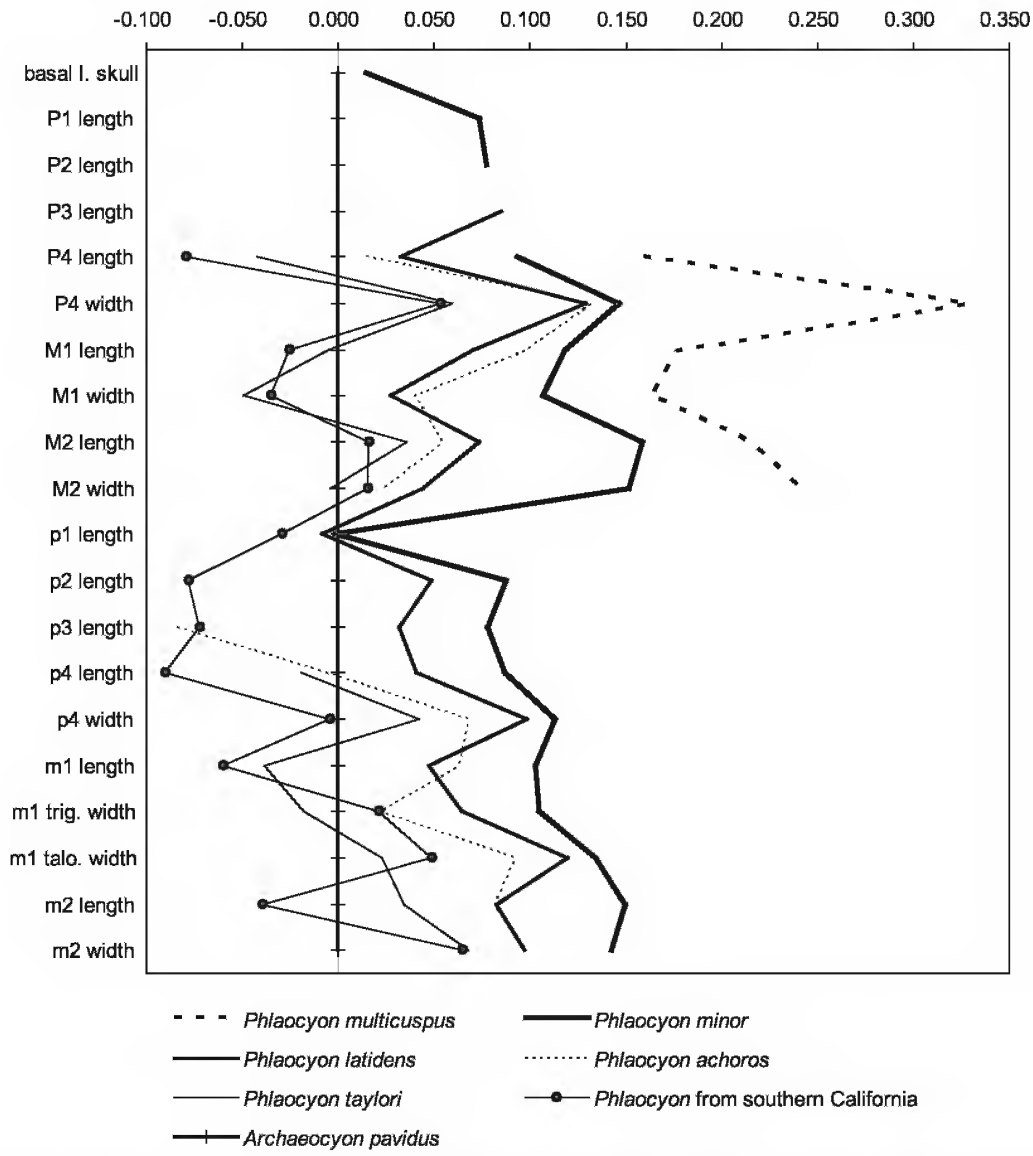

Figure 5 Log-ratio diagram for dental measurements of select species of *Phlaocyon* using *Archaeocyon pavidus* (Stock, 1933) as a standard for comparison (straight line at zero). See Table 2 for actual measurements.

lower canine (UF 163741) in Hayes' original hypodigm. This canine has numerous fine grooves along the shaft that are completely absent in LACM 148401. Other known *Phlaocyon* specimens also lack such fine grooves.

Besides the above-mentioned misidentification of an upper canine, the rest of the Florida hypodigm for *P. taylori* appears to be correctly assigned. Although isolated teeth represent all of the Brooksville 2 Local Fauna *Phlaocyon* material collected by screen washing, the small pockets of the fissure-fill deposits from which the collections came seem to indicate that the Florida *Phlaocyon* teeth probably represent a relatively uniform sample of limited geographic and chronologic distribution (Hayes, 2000). By comparison, the California material might come from somewhat different horizons, as shown in the slight morphological disparity between the upper and lower teeth. For example, compared with the Florida material, the upper teeth (LC 9112 and LC 9114) from California show a broader P4, usually a derived character in *Phlaocyon*, whereas the California lower teeth (LACM 148401) have a weaker development of the protostylids on lower molars, a more primitive feature. Such variation

Table 3 Data matrix (12 taxa and 26 characters) for cladistic analysis of species of *Phlaocyon*. Coding for *P. taylori* is based on composite materials from Florida and California and, for other taxa, follows Wang et al. (1999). Certain characters (e.g., size and proportions of premolars) are probably not fully independent within the *Phlaocyon* clade, but remain separately coded because they often vary independently within the Borophaginae as a whole. Character numbers (in parentheses) and polarities are as follows (see Wang et al. [1999] for detailed descriptions of individual characters): (1) rostrum length, 0 = unshortened, 1 = shortened; (2) frontal sinus, 0 = absent, 1 = present; (3) zygomatic scar, 0 = wide, 1 = narrow; (4) I3 size, 0 = small, 1 = enlarged; (5) canine crown lateral groove, 0 = absent, 1 = present; (6) premolar cusplets, 0 = well developed, 1 = reduced; (7) premolar high crowned, 0 = no, 1 = yes; (8) premolars shortened, 0 = no, 1 = yes; (9) premolar width, 0 = narrow; 1 = widened; (10) upper molar enlargement, 0 = no, 1 = yes; (11) P4 protocone, 0 = small, 1 = large; (12) P4 parastyle, 0 = absent, 1 = weakly developed; (13) P4 lingual cingulum, 0 = narrow, 1 = widened, 2 = formation of hypocone; (14) M1 shape, 0 = transversely wide, 1 = transversely narrow; (15) M1 metaconule, 0 = small, 1 = large, 2 = extra labial cuspule; (16) M1 internal cingulum, 0 = ridgelike, 1 = conical (to form a hypocone); (17) M1 paraconule, 0 = absent or weak, 1 = distinct; (18) M2 internal cingulum, 0 = ridgelike, 1 = cusplike; (19) M2 metaconule, 0 = isolated, 1 = connected to posterior cingulum; (20) p1, 0 = present, 1 = absent; (21) m1 protostylid, 0 = absent, 1 = small, 2 = large; (22) m1 talonid cusps, 0 = crestlike, 1 = conical, 2 = with transverse cristids; (23) m1 talonid, 0 = narrow, 1 = widened; (24) m2 enlargement, 0 = not enlarged, 1 = enlarged; (25) m2 reduction, 0 = not reduced, 1 = reduced; (26) m2 protostylid, 0 = absent, 1 = small, 2 = large.

	12345	1 67890	11111 12345	11112 67890	22222 12345	2 6
Archaeocyon pavidus	00001	00000	00000	00000	00000	0
Rhizocyon oregonensis	00000	00000	00010	00010	00000	0
Phlaocyon minor	00000	00101	00011	00010	10110	0
P. latidens	000??	00101	00111	10010	10110	0
P. annectens	10?00	10101	00111	10010	11100	0
P. taylori	????0	10101	10112	11010	11100	1
P. achoros	1????	10101	11212	1101?	11100	1
P. multicuspus	0100?	??101	11212	1111?	?????	?
P. marslandensis	11111	?1101	10211	10010	12100	1
P. leucosteus	10111	11101	10211	10010	12100	2
P. yatkolai	1???0	1001?	?????	????1	02100	0
P. mariae	1????	10010	1?201	10?1?	?2101	0

could result from a somewhat older age for the Lower Bowerman Landfill locality relative to the FTC/Oso locality (see "Geology, Age, and Associated Fauna" section above).

PHYLOGENETIC COMMENTS. As pointed out by Hayes (2000), *P. taylori* shares with another Florida Arikareean species, *Phlaocyon achoros* (Frailey, 1979), and a northern Great Plains species, *Phlaocyon multicuspus* (Romer and Sutton, 1927), an accessory cuspule next to the metaconule on its upper molars, a unique character that is present only in these three species. Wang et al. (1999) further identified additional dental characters supporting such a clade: presence of a P4 parastyle and a distinct M1 paraconule. A cladistic analysis incorporating *P. taylori* places it at the base of a *taylori–achoros–multicuspus* clade (Table 3, Fig. 6). The position of *P. taylori* in this new analysis provides a sense of transition within this clade and indicates an actual sequence of character evolution.

Recognition of *P. taylori* in early Arikareean age in Southern California presents some interesting implications about the chronology, zoogeography, and paleoenvironment of this species. Hayes (2000) placed the Brooksville 2 and Cow House Slough local faunas in the middle Arikareean. In a recent synthesis, Tedford et al. (2004) put the Brooksville 2 and Buda local faunas within their "Ar2" between 26 and 23 Ma. Being a small, hypocarnivorous carnivoran in the Arikareean, *Phlaocyon* is one of the earliest canids to occupy an ecological space similar to that of modern procyonids, as suggested long ago by Wortman and Matthew (1899), who pointed out the striking dental similarities between *Phlaocyon* and procyonids. As do living raccoons, the small *Phlaocyon* in the Arikareean of Florida might have preferred wooded areas in accord with its omnivorous diet. Presence of such forms in Southern California might suggest the existence of similar habitats at that time.

Tribe Borophagini (Simpson, 1945) Wang, Tedford, and Taylor, 1999

Desmocyon Wang, Tedford, and Taylor, 1999

Desmocyon thomsoni (Matthew, 1907)

Figure 7A and 7B; Table 4

REFERRED SPECIMEN. LC 7658, crushed cranial fragments with left and right bullae, erupting left P2, broken dP3, complete dP4,

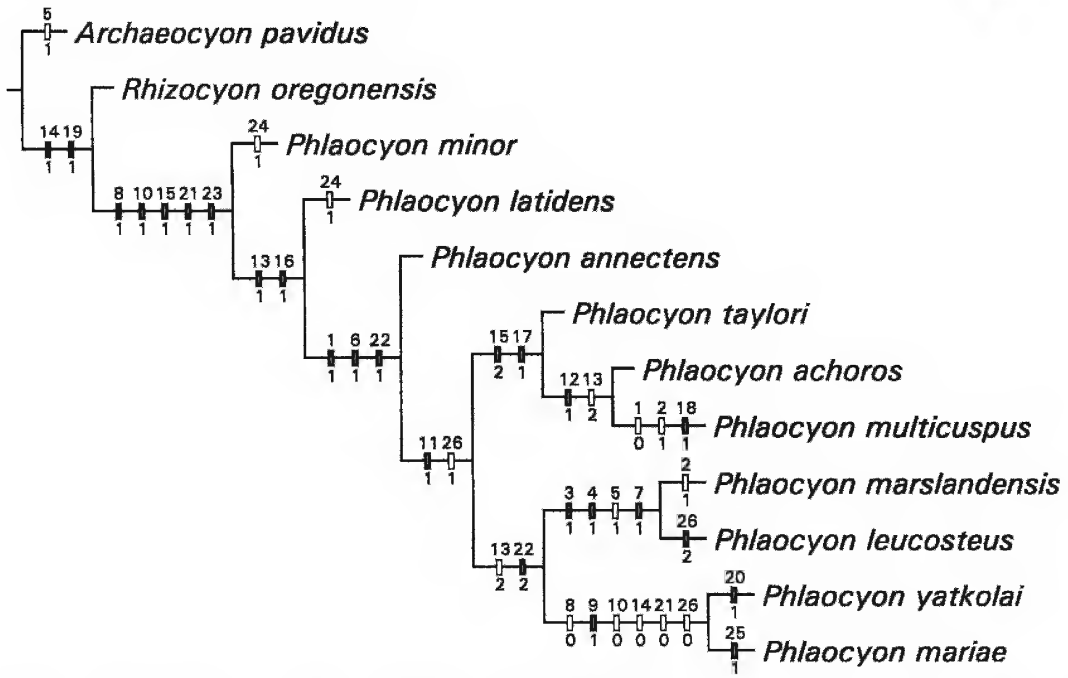

Figure 6 Phylogenetic relationships of species of *Phlaocyon* using *Archaeocyon pavidus* (Stock, 1933) and *Rhizocyon oregonensis* (Merriam, 1906) as outgroups. Branch and bound option in PAUP (version 3.1.1; Swofford, 1993) yields two shortest trees using data matrix in Table 3 (length = 40; consistency index [CI] = 0.75; retention index [RI] = 0.78), essentially the same two trees based on a matrix without *P. taylori* (Wang et al., 1999:fig. 138B). The relationship of *P. taylori* Hayes, 2000, with *P. achoros* (Frailey, 1979) and *P. multicuspus* (Romer and Sutton, 1927) remains the same in both trees. We arbitrarily chose the same topology as in Wang et al. (1999) to illustrate the character transformations. Characters in support of the *Phlaocyon* clade are not necessarily exclusively shared by species of *Phlaocyon* because of the omission of intermediate taxa between *Rhizocyon oregonensis* and *Phlaocyon minor* (Matthew, 1907). Solid bars indicate unique occurrences of synapomorphies, and open bars indicate homoplasies or reversals. Numbers above and below the bars correspond to character numbers and character states, respectively, in Table 3.

M1, and erupting right P4–M1. Field No. GC 93.24.22, in SE Borrow Site of the Santiago Canyon Landfill locality, LC locality 166, Orange County, California. Undifferentiated Sespe or Vaqueros formations, Hemingfordian age. Collected by Gino Galvano on 8 January 1993 (see further comments in "Geology, Age, and Associated Fauna" section above).

DESCRIPTION. Much of the cranium is too crushed and fragmented to be described. Part of the skull roof is preserved and shows a smooth surface with a sagittal crest, probably as a result of immaturity as indicated by its deciduous teeth. The two bullae are preserved, but they are extensively distorted.

The dP3 preserves only the posterior portion of the shearing blade behind the deciduous carnassial notch. Its anterior and lingual roots indicate its anteriorly expanded paracone and lingually positioned protocone, as is typical of deciduous carnassials of canids. The dP4 is completely preserved and suffers moderate wear in its talon basin. A triangular outline for the tooth is typical of deciduous P4s of canids. The paracone and metacone are about equal in size, and they are more marginally located and more toward the anterior and posterior corners of the tooth, respectively, than is the case for the permanent M1. The parastyle is very reduced but a metastyle is well developed posterior to the metacone and being almost as long as the metacone. The protocone is also very marginally located toward the lingual border, which leaves a large, shallow talon basin that shows appreciable wear against the hypoconid of the dp4. A very indistinct protoconule and metaconule are present, which are also somewhat worn. There is no lingual cingulum surrounding the protocone, as is present on the adult dentition (M1).

The left P4 is presumably still unerupted in the palate dorsal to the dP3–4. The right P4 is in a similar stage of eruption, but the dP4 is mostly missing, permitting the P4 to be fully exposed. The P4 is unworn. The paracone reclines backward and has two prominent, sharp ridges that originate from the base of the tooth. A larger

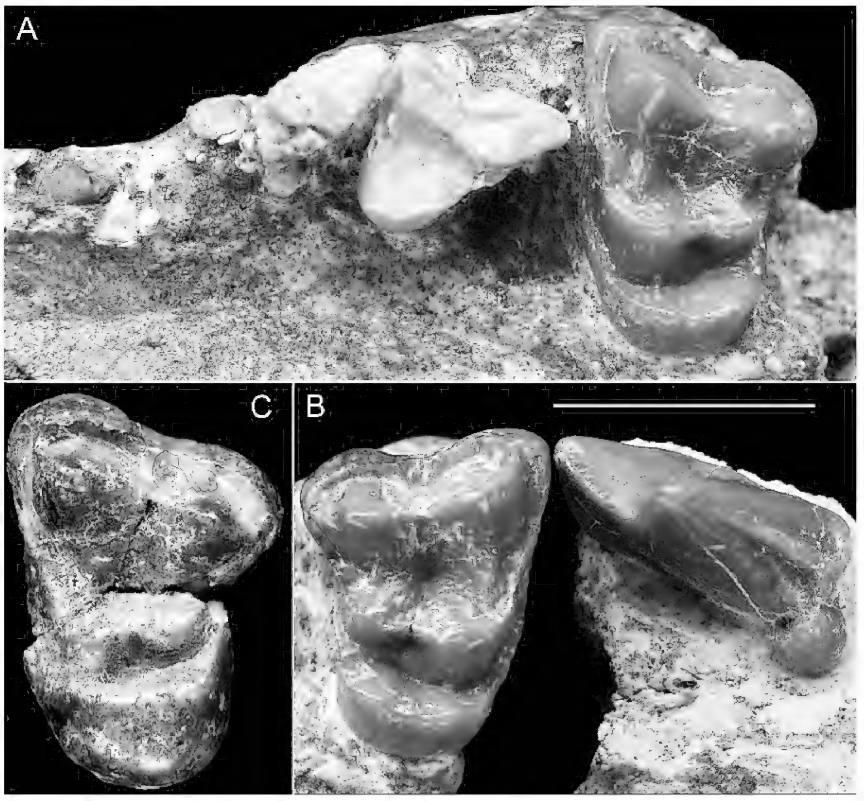

Figure 7 **A,** occlusal view of left P2 (erupting), dP3 (broken), dP4–M1 of LC 7658, *Desmocyon thomsoni* (Matthew, 1907); **B,** occlusal view of right P4–M1 of LC 7658, *Desmocyon thomsoni* (P4 and M1 created from composite images because of the different erupting stages of the two teeth); **C,** left M1 of *Metatomarctus canavus* (Simpson, 1932), LC 7692. Scale bar = 10 mm.

ridge is on the anterior face of the paracone and ends near the apex of the paracone. A smaller ridge immediately lingual to the anterior ridge terminates about midway along the paracone; it is connected to the base of the protocone. The anterior ridge widens at the base to form a triangular facet facing anteriorly, as is typical for mesocarnivorous borophagines. This triangular facet is very weakly notched toward the ventral tip, indicating the formation of a small parastyle. The conical P4 protocone is retracted slightly toward the main body of the paracone; thus, it might appear to be slightly less salient than it originally was. A distinct lingual cingulum is present along the entire length of the lingual border of the tooth.

The left and right M1s are perfectly preserved. Although fully erupted, they have suffered no discernable wear. The sizes and heights of the metacone and paracone are almost identical, although the paracone has a more prominent lingual ridge near its base. The protocone is about the same size and height as the paracone, followed posteriorly by a slightly smaller metaconule. The lingual cingulum (hypocone) surrounds the protocone and metaconule, although the anterior segment tapers off along the anterior facet of the protocone. There are indistinct notches along the crest of the lingual cingulum.

Table 4 Dental measurements (mm) of *Desmocyon thomsoni* (Matthew, 1907) from Southern California, the holotype from South Dakota, and the means of specimens from South Dakota, Wyoming, Nebraska, Oregon, and New Mexico after Wang et al. (1999:appendix III).

	Southern California LC 7658	South Dakota AMNH 12874	Mean (n = 30–33)
dP3 length	8.5*		
dP3 width	4.5*		
dP4 length	7.2		
dP4 width	7.0		
P4 length	12.3	13.0	12.05
P4 width	6.4	7.0	6.00
M1 length	9.8	10.5	9.54
M1 width	12.2	12.8	11.89

* Estimated.

Table 5 Dental measurements (mm) of *Metatomarctus canavus* (Simpson, 1932) from Southern California and the means of specimens from Florida, Delaware, Nebraska, Wyoming, and New Mexico after Wang et al. (1999:appendix III).

	Southern California LC 7692	Mean (n = 35–36)
M1 length	11.2	11.77
M1 width	14.0	14.51

COMPARISONS. The dental morphology of LC 7658 is that of a typical mesocarnivorous borophagine, with a reduced parastyle, a well-developed metaconule, and a lingual cingulum that surrounds the entire protocone and metaconule. The dimensions of the P4 in LC 7658 are similar to those of *Paratomarctus kelloggi* (Merriam, 1911), but the M1 lacks the corresponding enlargement in a hypocarnivorous form such as the latter. Although LC 7658 is also comparable in size to *Microtomarctus conferta* (Matthew, 1918), its lack of a fully developed parastyle on the P4 is in sharp contrast to the presence of this structure in *M. conferta*. Furthermore, the M1s in *M. conferta* tend to be more quadrate than in the somewhat transversely elongated outline in LC 7658.

Within the paraphyletic genus *Desmocyon*, *Desmocyon matthewi* Wang, Tedford, and Taylor, 1999, also has similar dental dimensions to LC 7658. *Desmocyon matthewi* is mainly diagnosed on the basis of slightly more derived cranial morphology (domed forehead and connection of the premaxillary and frontal) and a transverse cristid between hypoconid and entoconid of the m1, characters that are not preserved on LC 7658. Our decision to assign this specimen to *D. thomsoni* is thus somewhat arbitrary, and it is mainly based on the slightly smaller size of the latter, which is more consistent with LC 7658.

This is the first report of this species in California. Neither species of *Desmocyon* has previously been recorded in California, although the smaller and more primitive *D. thomsoni* is more widespread and has a longer geologic range than *D. matthewi* (see Wang et al., 1999). *Desmocyon thomsoni* is present in the John Day Formation of Oregon, but it is represented by only a maxillary fragment with M1–2 (AMNH 7238).

Metatomarctus Wang, Tedford, and Taylor, 1999

Metatomarctus canavus (Simpson, 1932)
Figure 7C; Table 5

REFERRED SPECIMEN. LC 7692, isolated left M1, field No. GC 93.24.121, collected by Gino Galvano on 13 May 1993, in SE Borrow Site of the Santiago Canyon Landfill locality, LC locality 166, Orange County, California. Undifferentiated sediments of Sespe or Vaqueros formations, Hemingfordian age. (see further comments in "Geology, Age, and Associated Fauna" section above).

DESCRIPTION. LC 7692 suffers from breakage across the middle, resulting in a small gap (missing enamel) near the posterior end of the break. The paracone in LC 7692 is slightly larger and taller than the metacone, and the protocone is slightly larger than the metaconule. A labial cingulum is well developed along the entire length of the paracone–metacone. The lingual cingulum (hypocone) surrounds both the protocone and metaconule. The cingulum has a transversely broad base and occupies a much larger area than the protocone and metacone combined. The cingulum is also taller than the protocone.

COMPARISONS. LC 7692 is clearly a borophagine canid because of its large metaconule, reduced parastyle area, and a rather anteriorly located lingual cingulum (hypocone), characters that are in contrast to the much reduced metaconules, large parastyles, and posteriorly located lingual cingulum in hesperocyonines (Wang, 1994). Among medium-sized mesocarnivorous borophagines, LC 7692 compares best with *M. canavus* in size, overall proportions (transversely long), and a thickened lingual cingulum, although caution needs to be exercised when identifying such meager material. A larger size (by 15%), more transversely elongated proportion, and a broader lingual cingulum are features that easily distinguish LC 6792 from *D. thomsoni* from the same locality (LC loc. 166).

Subfamily Caninae Fischer de Waldheim, 1817

Leptocyon Matthew, 1918

Leptocyon vulpinus (Matthew, 1907)
Figure 8; Table 6

REFERRED SPECIMEN. LC 9113, maxillary fragment with left P4–M1, FTC/Oso locality, LC locality 202, 33°36′03″N, 117°36′52″W, Orange County, California (see further comments in "Geology, Age, and Associated Fauna" section above).

DESCRIPTION. The maxillary fragment preserves the floor of the orbit and the ventral border of the infraorbital canal. The P4 is slender and elongated. Only a small anterior cingulum is present. There is no labial cingulum, whereas the lingual cingulum is weakly developed and restricted to the posterior half of the tooth. A distinct protocone is located anterior to the anterior border of the paracone, such that the apex of the protocone is at the same level as the anterior border of the paracone. The protocone is conical without a surrounding cingulum. The

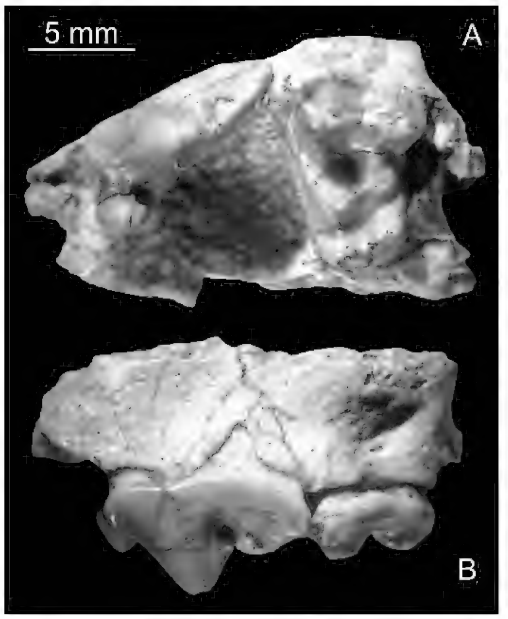

Figure 8 *Leptocyon vulpinus* (Matthew, 1907), upper teeth, LC 9113, FTC/Oso locality, LC locality 202, Orange County, California: **A,** occlusal view; **B,** lateral view.

paracone has a faint anterior ridge leading to the anterior cingulum.

The M1 is labiolingually narrow. The parastyle area is reduced, such that the labial cingulum has a uniform width around both the paracone and metacone. The paracone is slightly larger than the metacone, and these two cusps are connected by a ridge. The protocone is crestlike. Wear on the preprotocrista makes the paraconule indistinct, whereas the metaconule is still clearly visible, which expands lingually from the postprotocrista. The internal cingulum is narrow and surrounds the protocone. The anterior segment is much thinner than the medial segment. The internal cingulum is also divided by a small notch at a level just posterior to the protocone.

The M2 is represented by the anterior labial and lingual alveoli, which indicate that the M2 is not enlarged.

COMPARISONS. Among early canids, LC 9113 is easily distinguishable from members of the Hesperocyoninae by its anteriorly located P4 protocone, reduced parastyle on the M1, narrow lingual cingulum of M1 that does not swell posterolingually, and a distinct metaconule. These characters indicate that LC 9113 belongs to the Borophaginae–Caninae clade. Morphological differences between basal borophagines and canines are subtle, and for lack of more diagnostic teeth, LC 9113 is here placed with the Caninae mainly on the basis of dental proportions: a transversely narrow and elongated P4 and transversely elongated M1.

Table 6 Dental measurements (mm) of *Leptocyon vulpinus* (Matthew, 1907) from Southern California and the holotype from South Dakota.

	Southern California LC 9113	South Dakota AMNH 12883
P4 length	9.8	10.4
P4 width	4.3	4.4
M1 length	7.1	8.5
M1 width	9.4	

Late Oligocene and middle Miocene basal Caninae are represented by a series of small fox-sized forms in the genus *Leptocyon* (Tedford et al., 1995, in press). Among early *Leptocyon* of Arikareean and Hemingfordian age, LC 9113 falls within the size range of *L. vulpinus* (Table 6). A noticeable difference is the anteroposteriorly short M1 in LC 9113, here tentatively interpreted as a geographic variation. Following Matthew's (1907) original description of *Nothocyon vulpinus* from the "Lower Rosebud" beds of South Dakota, the holotype had remained the only specimen of this species to include upper teeth, prior to the present description of LC 9113.

CONCLUSIONS

1. Six species of fossil dogs, representing three subfamilies of Canidae were collected from Southern California during paleontologic resource mitigation activities. These can be identified as ?*Mesocyon* sp., *Cynarctoides whistleri* sp. nov., *Phlaocyon taylori*, *Desmocyon thomsoni*, *Metatomarctus canavus*, and *Leptocyon vulpinus* from the Arikareean through Hemingfordian parts of sediments referred to as the undifferentiated Sespe/Vaqueros formations.
2. We name the new species, *C. whistleri*, from California and Texas. Its combination of primitive and derived characters indicates that it is a transitional form, probably in isolation from the main theater of evolution for *Cynarctoides* in the northern Great Plains.
3. The specimen that we identify as *P. taylori* is the first record of this species outside of Florida, and the Southern California material substantially improves our knowledge of this small canid.
4. The coyote- to fox-sized canids *Mesocyon*, *Desmocyon*, *Metatomarctus*, and *Leptocyon* were previously known from the Great Plains, and their presence in California indicates wide distributions for these cursorial forms.

ACKNOWLEDGMENTS

We take great pleasure in dedicating this paper to Dr. David P. Whistler, Curator Emeritus of Vertebrate Paleontology at the Natural History Museum of Los Angeles County. David was instrumental in the acquisition and study of the Bee Canyon Landfill Fauna and other Southern California late Cenozoic vertebrate fossils. Discussions with David Whistler and E. Bruce Lander helped to clarify the geologic and faunal context of the specimens that are described here. We also thank Bruce Lander for providing unpublished manuscripts on the local stratigraphy. Howell Thomas prepared the specimens described here. Richard Meier took the photographs for Figure 3. We thank Lisa C. Babilonia, John D. Cooper, and Mark A. Roeder for access to and loans of specimens from the LC and OCPC. We are indebted to Robert M. Hunt, Jr., Annalisa Berta, Hugh M. Wagner, Lawrence G. Barnes, and John M. Harris for their critical reviews that greatly improved this paper. This research was supported in part by grants from the National Science Foundation (DEB-9420004, DEB-9707555, EAR-0446699).

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Metalopex, a new genus of fox (Carnivora: Canidae: Vulpini) from the late Miocene of western North America

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ABSTRACT. Late in the Clarendonian (early late Miocene, ~10 Ma), the subfamily Caninae (which contains all extant canids), experienced its first major radiation. This phase yielded the tribes comprising the foxes, wolves, and South American canids. We describe here a new extinct genus in the tribe Vulpini, *Metalopex*, which appeared at that time. *Metalopex,* in the late Clarendonian to early Hemphillian, was the earliest and only member of the Vulpini until its sister taxon *Urocyon* and the early species of *Vulpes* appeared at the beginning of the Hemphillian (9 Ma).

INTRODUCTION

The fossil mammals of the Great Basin of California and Nevada and the Columbia Plateau of Oregon were of great interest to John C. Merriam and his student Chester Stock, and the latter brought that fascination with him on his appointment to the new staff of the California Institute of Technology (CalTech) in 1926. Stock and his students continued the exploration of these western regions for more than 20 years, and they accumulated at CalTech a large collection, replete with many type specimens. These fossils were mostly described in the pages of the Carnegie Institution of Washington, *Contributions in Paleontology* series. After Stock's death in 1950, the Natural History Museum of Los Angeles County (LACM) acquired the collection. With Dr. David P. Whistler's appointment as Curator of Vertebrate Paleontology at LACM in 1970, the tradition of Great Basin studies continued at this institution. We offer the following description of a Great Basin carnivoran in honor of David Whistler's retirement and to call attention to his contributions to the long chain of studies on the paleofaunas of far western North America.

Before the Clarendonian of North America, the Caninae, the subfamily containing all living canid species, was represented solely by species of the extinct genus *Leptocyon* Matthew, 1918. For the first 20 Ma of canine history, this subfamily showed limited diversity (Tedford et al., in press). Evidence of the first burst of diversification appears early in the late Miocene (~10 Ma), with the appearance in the record of representatives of both the Tribe Vulpini and Canini. By the beginning of the Hemphillian (9 Ma), *Vulpes* Frisch, 1775, joins the new genus described below in representing the Vulpini, whereas the Canini are represented by *Eucyon* Tedford and Qiu, 1996.

ABBREVIATIONS

F:AM	Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York USA
IMNH	Idaho Museum of Natural History, Pocatello, Idaho USA
LACM	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA
LACM (CIT)	California Institute of Technology Collection at the Natural History Museum of Los Angeles County, Los Angeles, California USA
UCMP	Museum of Paleontology, University of California at Berkeley, Berkeley, California USA
UNSM	University of Nebraska State Museum, Lincoln, Nebraska USA

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Canidae Fischer de Waldheim, 1817

Subfamily Caninae

Fischer de Waldheim, 1817

Tribe Vulpini Hemprich and Ehrenberg, 1832

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DISCUSSION. Members of this tribe are mostly small canids (foxes, zorros). They are distinguished from all other members of the subfamily Caninae by possessing a wide paraoccipital process that is broadly sutured to the posterior surface of the tympanic bulla with a short and laterally turned distal process, which usually does not extend below the ventral surface of the bulla. Species of the tribe Vulpini are distinguished from species of *Leptocyon* and united with those of the Canini by common possession of three synapomorphies: loss of the medial cusp of I3, loss of the entepicondylar foramen on the humerus, and reduction of metatarsal I and loss of its phalanges. Autapomorphies of the Vulpini include nasals that do not extend posterior to the maxillary–frontal suture; enlargement of the m2 metaconid so that it exceeds the protoconid in size, producing a convex lingual outline to the tooth; and further reduction of the M1 parastyle and loss of its union with the preparacrista. In a reversal relative to late *Leptocyon* species, but synapomorphic within the vulpines and canines, the M2 of *Metalopex* retains the primitive presence of a metaconule and postprotocrista.

Metalopex new genus

DIAGNOSIS. As for the monotypic species.

TYPE SPECIES. *Metalopex merriami* sp. nov.

ETYMOLOGY. Greek: *meta*, near, and *alopex*, fox.

DISCUSSION. *Metalopex* differs principally from both *Vulpes* and the *Urocyon* Baird, 1857, group in its unique M2, which lacks a postprotocrista but retains the metaconule; in retaining the primitive form of the upper incisors, in which I3 still has a medial cusp; in its relatively derived enlargement of the mastoid process; and in the uniquely enlarged m3, which retains the trigonid and talonid. Nevertheless *Metalopex* appears to be the sister taxon of *Urocyon*. They are united by such synapomorphies as m2 with elongate talonid (>90% of trigonid length); the M1 narrow for its length; and the presence of protostylids on m1 and m2, which is a unique feature.

The above features mark an early divergence within the Vulpini that gives rise to two clades: one that contains the *Vulpes* clade and the *Urocyon* clade that contains *Metalopex*. The former reached Eurasia near the beginning of the Pliocene (Qiu and Tedford, 1990), and the latter reached Asia and Africa in the early Pleistocene as *Prototocyon* Pohle, 1928 (*P. curvipalatus* (Bose), 1880, of the Upper Siwaliks of India and *Prototocyon recki* Pohle, 1928, of Olduvai Gorge, Bed I, Tanzania). In Africa, *Prototocyon* species gave rise to the living *Otocyon megalotis* (Desmarest, 1822) as an endemic taxon. In our previous analysis (Tedford et al., 1995) *Otocyon* Müller, 1836, has a sister relationship with *Urocyon*. Although a member of this clade, *Metalopex* is more basal and stands as a sister taxon to both *Urocyon* and *Otocyon*.

Metalopex merriami new species

Figure 1A–I; Tables 1 and 2

Tephrocyon, near *T. kelloggi*, Merriam 1911: 238.

Vulpes sp., Becker and McDonald 1998:33.

DIAGNOSIS. Derived features that distinguish *Metalopex* from *Vulpes* are: mastoid process large; M1 and M2 more quadrate in shape, anteroposteriorly long relative to width; M2 without postprotocrista; p2 isolated from longer diastemata than other premolars; m2 large relative to m1, more posteriorly extended anterolabial cingulum, and talonid longer relative to trigonid; m3 uniquely elongate, trigonid longer than talonid, that is, relatively large paraconid shelf and protoconid and metaconid situated more posteriorly.

Primitive characters retained by *Metalopex* include: marked depression on frontals adjacent to postorbital process, which denotes an absence of frontal sinus; basioccipital wide, bulla small, strong medial and lateral cusplets on I2 and medial cusplet on I3; M2 metaconule present despite reduction and loss of connecting postprotocrista; m1 talonid lacks transverse crest between entoconid and hypoconid, and also lacks hypoconulid; and m2 with paraconid or paracristid.

HOLOTYPE. F:AM 49282, partial cranium with alveolus of I3–M2, detached premaxillary fragment with I1–2, and left partial ramus with c alveolus–m3 (p1 alveolus and m1 broken), Figure 1A–D, F, G, from 3 miles (~5 km) north of Line Quarry, just north of the Oregon–Nevada boundary line, Thousand Creek Formation (early Hemphillian), Harney County, Oregon.

REFERRED MATERIAL. From near the type locality, Thousand Creek Formation (early Hemphillian), Humboldt County, Nevada: F:AM 61016, partial left ramus with m1 and m2–m3 both broken (Fig. 1E). From UCMP Locality 1103, Thousand Creek Formation, Humboldt County, Nevada: UCMP 12542 right m2 (Merriam, 1911:fig. 7).

From Mitchell Road, UCMP Locality V4825, Rattlesnake Formation (early Hemphillian), Wheeler County, Oregon: UCMP 41084, isolated left M1 and M2.

From Star Valley, IMNH locality 67001, sediments interbedded with Banbury Basalt (early Hemphillian), Owyhee County, Idaho: IMNH 24584, partial right ramus with p4–m2; IMNH 27866 partial left ramus with c, p1–4; IMNH trigonid of left m1 (Becker and McDonald, 1998).

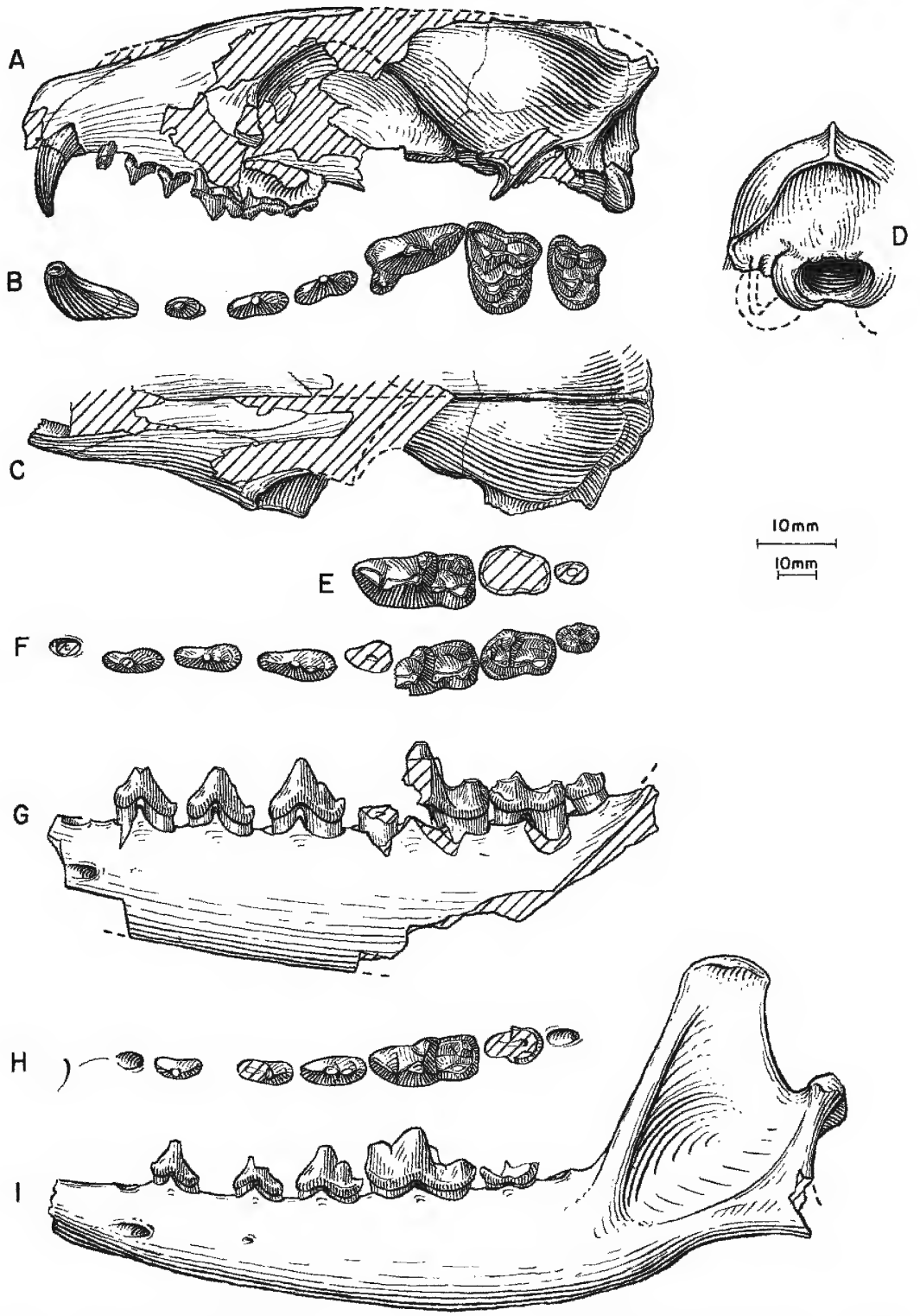

Figure 1 *Metalopex merriami* gen. et sp. nov., early Hemphillian, Oregon, Nevada, and Nebraska. **A–D,** Type skull, F:AM 49282: **A,** lateral view, reversed; **B,** occlusal view, reversed; **C,** dorsal view, from both sides; **D,** occipital view, reversed. **E,** Ramal fragment, F:AM 61016,occlusal view. **F–G,** Ramus, F:AM 49282: **F,** occlusal view; **G,** lateral view. **H–I,** Ramus, UNSM 26098: **H,** occlusal view, reversed; **I,** lateral view, reversed.

Table 1 Measurements (mm) of upper dentition of *Metalopex merriami* gen. et sp. nov.

	F:AM 49282*	UCMP 41084	UNSM 419-47	UNSM 522-47
LP2	7.8	—	—	7.6
LP3	8.5	—	—	8.9
LP4	13.5	—	—	—
WP4	5.0	—	—	—
LM1	10.7	9.9	11.3	—
WM1	11.4	10.9	11.8	—
LM2	8.1	7.4	7.5	—
WM2	9.3	9.6	8.2	—

L, length or anteroposterior diameter; W, width as transverse diameter with the use of standard reference points (Wang et al., 1999).
* Holotype.

From Kern River, LACM (CIT) locality 49, Kern River Formation (early Hemphillian), Kern County, California: LACM 55217, partial left ramus with c (alveolus)–m2 (p1 alveolus, p2 broken and p3–4 alveoli).

From Gabaldon Badlands, 4 miles (~6 km) south of Rio Puerco station (late Clarendonian or early Hemphillian), Valencia County, New Mexico: F:AM 107607, two fragments of right ramus with c–p2 all alveoli, p3, p4 root, and m1–2 both broken (Lozinsky and Tedford, 1991:25, fig. 18D).

University of Nebraska State Museum locality Ft-48 (early Hemphillian), Ash Hollow Formation, Frontier County, Nebraska: UNSM 26135, left premaxilla with I1–3, right and left ramal fragments with c alveolus–p4; UNSM 521-47, partial left ramus with c alveolus, p1, p2–3 both broken, p4 root and m1–3 alveoli; UNSM 26136, left m1; UNSM 52247, left maxillary fragment with P2–3, protocone root of P4; and UNSM 419-47, right maxillary fragment with M1–2. From locality Ft. 49: UNSM 26098, right ramus with c–p1 alveoli, p2–m1 (p2 broken), m2 broken and m3 alveolus (Fig. 1H and 1I).

AGE AND DISTRIBUTION. Latest Clarendonian or early Hemphillian of New Mexico; early Hemphillian of California, Idaho, Nevada, Oregon, and Nebraska.

ETYMOLOGY. Named for John C. Merriam, pioneering vertebrate paleontologist of western America.

DESCRIPTION AND COMPARISONS. In the holotypic skull (F:AM 49282), the premaxilla, maxilla, nasals, and frontals are incomplete, and the basicranial area is crushed and broken. The skull is elongate, larger than that of *Vulpes stenognathus* Savage, 1941, and approximates the size of *Eucyon davisi* (Merriam, 1911). Unlike *Vulpes*, the contour of the maxillary surface above P1–3 is convex, as in *E. davisi*. Furthermore, the skull differs from that of *V. stenognathus* and is similar to that of *E. davisi*, in the wider and more arched palate and the greater dorsoventral height of the maxilla. Unfortunately the frontals are broken, obscuring the maxillary–frontal suture, but the remnants do not contradict the extension of the suture beyond the posterior end of the nasals. A fragment of the frontal with the postorbital process shows the primitive frontal depression adjacent to the process as in *Vulpes*. Moreover, the frontal fragment also reveals that *M. merriami* lacks the frontal sinus that is present in *Eucyon*. Enough of the frontals are present to show that the temporal crests join anterior to the parietal suture to form a moderately low sagittal crest similar to that in both *V. stenognathus* and *E. davisi*. The supraoccipital shield is broad, with the inion broader than in *V. stenognathus* and similar to that of *E. davisi*. The foramen magnum and occipital condyles are larger than in *V. stenognathus* and *E. davisi*, and the mastoid process is knoblike and enlarged as in members of the Canini. Although the basioccipital area is badly broken, it appears to have been relatively wider than in both *V. stenognathus* and *E. davisi*, and the broken tympanic bullae show that the bullae were small relative to the size of the skull.

Table 2 Measurements (mm) of lower dentition of *Metalopex merriami* gen. et sp. nov.

	F:AM 49282*	F:AM 61016	LACM 55217	IMNH 24584	IMNH 27886	UNSM 26098	UNSM 26135	UNSM 26136	UCMP 12542
Lp2	8.0	—	5.8	—	6.9	6.2	8.0	—	—
Lp3	8.6	—	7.0	—	7.9	7.0	8.4	—	—
Lp4	9.8	—	7.6	8.5	9.2	8.5	9.6	—	—
Wp4	4.0	—	—	3.3	3.5	3.6	4.0	—	—
Lm1	15.5	15.6	13.5	14.6	—	13.9	—	14.2	—
Wgm1	—	6.0	5.3	5.0	—	5.2	—	5.1	—
Wdm1	6.1	6.4	6.2	5.4	—	5.4	—	5.3	—
Lm2	9.5	10.0	9.0	8.8	—	7.8	—	—	10.0
Wm2	5.5	—	5.4	5.5	—	—	—	—	5.5

L, length or anteroposterior diameter; W, width or transverse diameter; Wg, width of trigonid m1; Wd, width of talonid, m1, with the use of standard reference points (Wang et al., 1999).
* Holotype.

A premaxillary fragment (UNSM 26135) has an unworn I2 and I3. The I2 has a well-developed medial and lateral cusplet, and the I3 has a well-developed medial cusplet but no lateral cusplet. Both incisors have a lingual cingulum, and there is a broad lingual shelf on I3. The complexity of the upper incisors exceeds that of *E. davisi*, *Leptocyon vafer* (Leidy, 1858), and *V. vulpes*, but the I3 is not enlarged as it is in the Canini. Compared with both *V. stenognathus* and *E. davisi*, the P1–3 are smaller relative to the length of the carnassial, more widely spaced, more slender, anteroposteriorly shorter, and taller crowned. They also lack accessory cusps, but the P3 has a posterior cingular cusp. Morphologically, the P4 closely resembles that of *V. stenognathus* and *E. davisi*, with the anterior border slightly notched because of the projection of the anterobuccal corner and the strong anteriorly directed protocone. The P4, however, is smaller relative to the molars than in both of the above, and it is more slender than that of *E. davisi*. Unlike *V. stenognathus* and *E. davisi*, the M1 and M2 in *M. merriami* are quadrate in shape, being anteroposteriorly long relative to their width. They are relatively low crowned, the labial border is strongly indented between the paracone and metacone, and there is a prominent buccal cingulum. The protocone of M1 is relatively large, and a postprotocrista extends to a well-developed metaconule. The hypocone is a long and ridgelike swelling of the posterolingual cingulum that ends posteriorly at the metaconule and extends anteriorly to join the anterolingual cingulum across the protocone to the base of the paracone. The M2 of *M. merriami* is even more quadrate than the M1, and the metaconule is present, but there is no postprotocrista connecting it with the protocone. As in the M1, the lingual cingulum from the M2 hypocone extends posteriorly to the metaconule and anteriorly to the paracone.

In *M. merriami*, the p2–4 are slender and tall-crowned for their length, and only p4 consistently possesses a posterior cusp. The p2 is isolated from the adjacent premolars by larger diastemata, as in species of the *Urocyon* group. Compared with *V. stenognathus* and *E. davisi*, the m1 is relatively short and robust, with the trigonid shorter relative to the length of the tooth. Furthermore, the paraconid is more oblique and the metaconid is larger and higher relative to the height of the protoconid than in either of these taxa. The m1 talonid is broad, with a relatively low and nearly subequal entoconid and hypoconid. Allowing for wear, the hypoconid is still smaller and lower crowned than that of both *V. stenognathus* and *E. davisi*. The m2 is elongate and larger relative to the length of the m1 than that of *V. stenognathus* and *E. davisi*. A well-developed anterolabial cingulum extends posteriorly across the protoconid and ends on the anterior face of the hypoconid. The m2 trigonid is elongate, with a paraconid that is larger than that of *V. stenognathus* and larger than that usually found in *E. davisi*. The protoconid and metaconid are situated more posteriorly than in *V. stenognathus*, with the larger metaconid situated posterior to the protoconid. Compared with both *V. stenognathus* and *E. davisi*, the m2 talonid is relatively longer and wider. In *M. merriami*, the m3 is also larger and more elongate than that of both *V. stenognathus* and *E. davisi*. Uniquely, the protoconid and metaconid are distinct subequal cusps that are situated more posteriorly than those of *V. stenognathus* or *E. davisi*, and the trigonid is longer than the talonid.

DISCUSSION. Size and morphology vary considerably within and between the local samples we identify as *M. merriami*. The fragmentary materials from UNSM locality Ft-48, for example, pertain to four individuals, two of which (UNSM 26098 and 26135) can be usefully measured and are indicated in Tables 1 and 2. The measured specimens are at the extremes of size variation in the dimensions of the lower dentition. The additional materials from the same locality fall between the measured values, indicating nearly continuous variation. The larger end of the range clearly overlaps the holotype of *M. merriami* (UNSM 522-47 includes alveoli of M1–2, and these are the size of F:AM 49282). We therefore have referred this material to *M. merriami*.

CONCLUSIONS

1. A new genus and species of fox, *Metalopex merriami*, defined here, is rare in fossil deposits but appears to have been widespread in western North America and in the Great Plains in the later Clarendonian and early Hemphillian (8–10 Ma). *Metalopex merriami* is similar in size to its sister vulpine, *Vulpes stenognathus*, and to the earliest canine, *Eucyon davisi*, which together represent an early phase in the history of the clades that contain the living foxes and wolves. At that time, the borophagine canids (Wang et al., 1999) were beginning their decline in diversity and only species of large body size remained, and this might have released ecospace to small- to medium-sized generalist canids.
2. The earliest appearance of the Vulpini and Canini in the late Clarendonian provides a minimum date of about 10 Ma for this divergence, a time that is not very far removed from the molecular estimates of 12.5 Ma (Bininda-Emonds et al., 1999) on the basis of living representatives.

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Genyonemus whistleri new species, a late Miocene sciaenid fish from California

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ABSTRACT. A new species of sciaenid fish, *Genyonemus whistleri* sp. nov., from the late Miocene Puente Formation of Southern California is described on the basis of a nearly complete articulated skeleton with an incomplete right saccular otolith *in situ*. Preservation of otoliths *in situ* with articulated fossil fish skeletons is rare and allows better correlation of taxa that are represented solely by articulated skeletal material and those that are identified only by isolated otoliths. This is the earliest known occurrence of the genus *Genyonemus* from the eastern Pacific realm and is the first fossil representative of the genus to be based on skeletal material. The associated ichthyofauna from the type locality of *G. whistleri* indicates a deep-water marine, lower mesopelagic environment. The presence of this presumably shallow water species in this deep-water deposit probably is the result of postmortem transport from a nearshore environment.

INTRODUCTION

The family Sciaenidae (croakers and drums) is a diverse group of perciform fishes comprising approximately 270 extant species that are assigned to approximately 70 genera (Nelson, 2006). This family inhabits primarily coastal marine and brackish water environments, with only a few species living solely in freshwater (Chao, 1978; Nelson, 2006). They are widely distributed in waters of the tropical and subtropical parts of the Pacific, Atlantic, and Indian oceans, and their diversity diminishes in more temperate waters (Druzhinin, 1974; Trewavas, 1977; Schwarzhans, 1993; Sasaki, 1996). Sciaenids are absent from the North Sea, and only a single species is recorded around southern Australia (Schwarzhans, 1993). They are also absent from around the Ryukyu Islands, New Zealand, and the Pacific Oceanic Island groups (Sasaki, 1989). This strongly suggests that the open ocean regions and cold extreme temperate zones were effective barriers to the distribution of this group.

Fossil sciaenids are preserved as articulated and semi-articulated skeletal remains, isolated scales, and otoliths. Articulated specimens are rare, but a relatively abundant fossil record based on otoliths extends back to the middle Eocene (e.g., Koken, 1888; Frizzell and Dante, 1965; Müller, 1999; Nolf, 2003).

The first reported fossil sciaenid from California, *Lompoquia retropes* Jordan and Gilbert, 1919, was based on a nearly complete skeleton from the late Miocene diatomites that are exposed near Lompoc in Santa Barbara County. David (1943) noted two more sciaenid taxa from these same late Miocene deposits at Lompoc: *Lompoquia culveri* (Jordan, 1925), and *Cynoscion* (*Aristoscion*) *eprepes* Jordan, 1921. David (1944) and Pierce (1956) reported isolated scales of *Lompoquia* Jordan and Gilbert, 1919, of Miocene age from California. The validity of recognizing two distinct species of *Lompoquia* from the deposits near Lompoc will require further study.

Fossil sciaenid otoliths were first recorded in California when Kanakoff (1956) reported six extant species from late Pleistocene deposits of Southern California. Otoliths referable to extant sciaenids have been reported subsequently from several other Pliocene and Pleistocene deposits in California (Fitch, 1964, 1967, 1968, 1970; Fitch and Reimer, 1967). Unidentified sciaenid otoliths have also been reported from early and middle Miocene deposits of central California (Mitchell and Tedford, 1973; Clarke and Fitch, 1979). More recently, two new species of sciaenids based on otoliths have been described from early Miocene deposits in central California and late Miocene deposits in Southern California (Huddleston and Takeuchi, 2006, 2007).

From August 1994 to November 1997, a fossil fish fauna consisting of articulated skeletal remains, skeletal remains with otoliths *in situ*, and isolated otoliths was recovered during earth-

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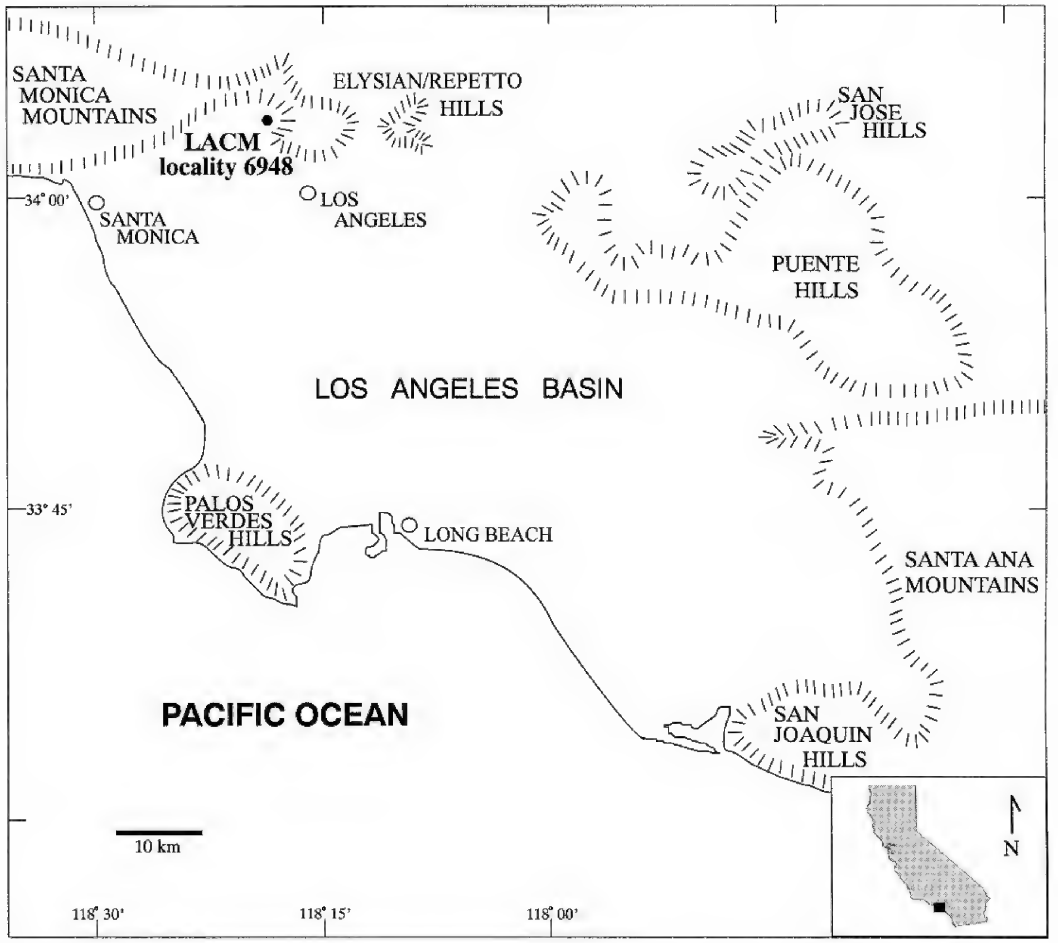


Figure 1 Map of the Los Angeles Basin showing the type locality, LACM locality 6948, of *Genyonemus whistleri* sp. nov.

moving activities that were associated with construction of a subway station for the Los Angeles County Metropolitan Transportation Authority (MTA) Metro Red Line. We here describe a new species of the sciaenid genus *Genyonemus* Gill, 1861, from this late Miocene locality, on the basis of a nearly complete skeleton that has an incomplete right saccular otolith *in situ*. This is the earliest geological occurrence of *Genyonemus* from the eastern Pacific realm.

LOCALITY AND GEOLOGY

The locality, Natural History Museum of Los Angeles County (LACM) locality 6948, is in the upper part of the Puente Formation (late Miocene) in the northern Los Angeles Basin, approximately 7 km northwest of downtown Los Angeles, California (Fig. 1). The site was discovered during construction of the MTA Metro Red Line subway station near the intersection of Vermont Avenue and Sunset Boulevard in the Hollywood District of Los Angeles, California. Fossils were recovered as part of a paleontological mitigation program for the MTA under the direction of an environmental consulting firm. Previously, no extensive marine faunas had been recovered from the Puente Formation in the northern Los Angeles Basin, partly because early urban development had obscured much of the surface in this area. Excavation at the Vermont/Sunset Station locality and other Metro Red Line subway station localities afforded the first opportunity to extensively sample subsurface strata in the upper part of the Puente Formation.

The upper part of the Puente Formation is composed of thinly bedded layers of light-gray to light-brown colored, silty clay shale, siltstone, and fine-grained sandstone. The estimated total thickness of the Puente Formation in the area is 960 m on the basis of surface and subsurface data (Dibblee, 1989). Only the upper 200 to 300 m of the shale layer was encountered during the

excavations mentioned above. This rock unit has been previously assigned to the Yorba Member of the Puente Formation by Schoellhamer (1954) and to the siltstone of the Puente Formation by Lamar (1970). Blake (1991), in a review of the biostratigraphy of the Neogene deposits of the Los Angeles Basin, designated as the Puente Formation in the subsurface of the Los Angeles Basin the stratigraphic interval that lies between the early to middle Miocene Topanga Formation and the early to late Pliocene Repetto Formation. Dibblee (1991, 1995), however, referred to this same unit as an "unnamed marine shale." The latter interpretation is variably accepted, and many workers continue to refer to these strata as the "Puente Formation." We follow Blake's (1991) stratigraphic terminology.

The principal outcrops of the Puente Formation, as have been recognized by various writers, are exposed around the northeastern and eastern margins of the Los Angeles Basin. Natland and Rothwell (1954) assigned the formation to the late Miocene "Delmontian" Benthic Foramineral Stage. Dibblee (1989) and Lamar (1970) reported upper Mohnian and lower "Delmontian" benthic foraminifera assemblages, with the upper Mohnian assemblages occurring in the lower 76 m of the shale unit. However, boundaries of benthic foraminiferal stages in the Cenozoic rocks of the Pacific coast of North America, and particularly within the Los Angeles Basin, have been shown to be unreliable age indicators by themselves because they are time-transgressive throughout much of the Neogene, relative to ages that have been derived from planktonic microfossils (Ponti et al., 1994; Prothero, 2001:389). A sediment sample from the Vermont/Sunset Station locality that was analyzed for microfossils was inconclusive. An additional sample from within the upper part of the Puente Formation, that was recovered at a nearby locality, LACM locality 6202 (Metrorail Wilshire/Vermont Station), provided an age of early late Miocene (Boettcher and Kling, 1993). Benthic foraminifera indicate an upper Mohnian Benthic Foraminiferal Stage (late Miocene), and calcareous nannofossils suggest assignment to zone CN9A. The siliceous microfossils indicate that the assemblage is no older than the uppermost part of the *Denticulopsis hustedtii* Zone.

METHODS AND MATERIALS

The holotype (LACM 144152) of *Genyonemus whistleri* sp. nov. was compared with dry skeletons, alcohol-preserved specimens, and otoliths of the Recent species *Genyonemus lineatus* (Ayres, 1855) that are housed in the Department of Ichthyology, LACM. Additional comparative material was observed at the Marine Vertebrate Collection, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California, and includes saccular otoliths of *G. lineatus*.

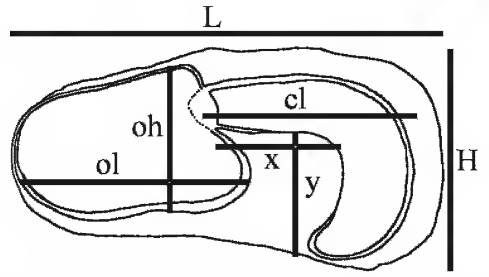


Figure 2 Line drawing of a generalized sciaenid right saccular otolith illustrating measurements used for proportional ratios: inner face view. **ABBREVIATIONS: H** = otolith height; **L** = otolith length; **cl** = cauda length; **oh** = ostium height; **ol** = ostium length; **x:y** = caudal curvature index (cci); modified after Schwarzhans (1993).

The holotype and other associated fossil fishes from LACM locality 6948 are catalogued and housed in the collections of the Department of Vertebrate Paleontology, LACM. Previously undisturbed strata and debris generated by earth-moving activities associated with construction were inspected for fossils by paleontologic construction monitors. The holotype of *G. whistleri* was discovered by splitting the shale along bedding planes, where it was mostly exposed in the field. Additional detailed preparation was done with the use of fine needles under a dissecting microscope.

Morphological terms used in the general description mainly follow those of Nolf (1985), Sasaki (1989), and Schwarzhans (1993). Meristic counts were made largely following Hubbs and Lagler (1964). Measurements and proportional ratios of the otoliths of the Sciaenidae (Fig. 2) follow the methods proposed by Schwarzhans (1993), and characters and their definitions for features of the saccular otolith are described below. Measurements used for proportional ratios on the inner face include the following: Otolith height (H) is the greatest dorsal to ventral height; otolith length (L) is the greatest anterior to posterior length; the measurement used for proportional ratios from lateral view is otolith thickness (T), which is the greatest inner face to outer face thickness taken in dorsal view; caudal length (cl) is measured from the dorsal edge of the cauda, at the dorsal caudal joint and extending to the posteriormost extension of the dorsal caudal margin; ostium height (oh) is the greatest dorsal to ventral height of the ostium with the otolith in natural position; ostium length (ol) is taken from the anterior edge of the ostium to the posteriormost extension of the ostium, including the postostial lobe if present; length of horizontal portion of the cauda (x) is measured from the caudal joint of the ventral caudal margin and

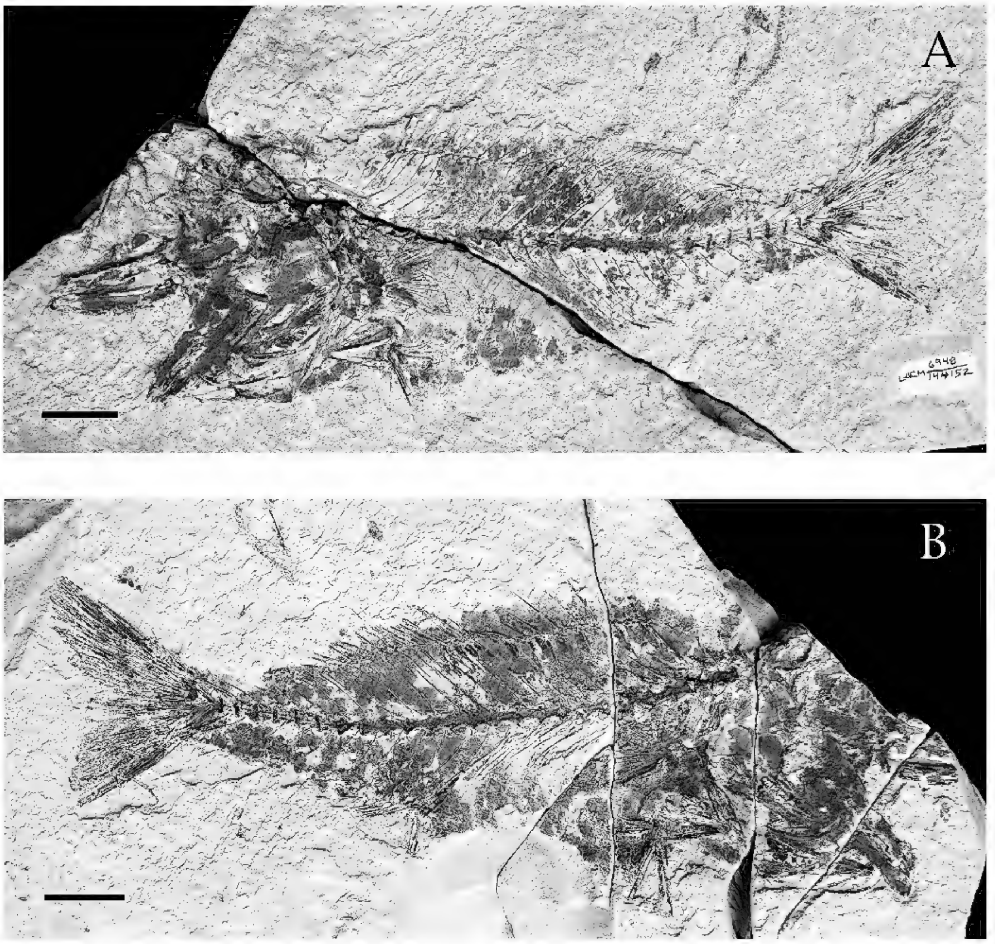


Figure 3 *Genyonemus whistleri* sp. nov., holotype, LACM 144152; estimated 191 mm standard length (SL): **A**, right counterpart; anterior end facing left; **B**, left counterpart; anterior end faces to the right. Scale bars = 2 cm.

extending to the posteriormost extension of the ventral caudal margin; length of down-turned portion of cauda (y) is from the highest point of the ventral caudal margin to the ventralmost point of the cauda termination.

SYSTEMATIC PALEONTOLOGY

Class Actinopterygii (*sensu* Nelson, 2006)

Division Teleostei (*sensu* Nelson, 2006)

Order Perciformes (*sensu* Johnson and Patterson, 1993)

Family Sciaenidae Cuvier, 1829

Subfamily Sciaeninae Gill, 1861

Genus *Genyonemus* Gill, 1861

Genyonemus whistleri new species

Figures 3–6; Tables 1–4

HOLOTYPE. LACM 144152, part and counterpart of a skeleton, lacking a portion of the skull, with an incomplete right saccular otolith *in situ*; collected by Michael W. Morris, 15 April 1997 (Fig. 3).

DIAGNOSIS OF SPECIES. A species of *Genyonemus*differing from *G. lineatus* by having the following combination of skeletal characters: more vertebrae (27; Table 1), fewer first dorsal fin spines (11 vs. 12–15 in *G. lineatus*; Table 1), and more slender vertebral centra. The saccular otolith of *G. whistleri* differs from that of other *Genyonemus* species by the following combination of characters: overall shape shorter and more rectangular, anterior cauda shorter and lacking a middorsal rise on the dorsal margin, ventral rim gently expanding more anteriorly, and posteroventral area indented and curved inward rather than rounded. The saccular otolith of *G. whistleri* differs from that of *G. lineatus* by having the postdorsal projection undeveloped and a greater standard length (SL)/otolith length (L) ratio (Table 2).

TYPE LOCALITY. LACM locality 6948, Metrorail Vermont/Sunset Station, Hollywood District, Los Angeles, Los Angeles County, California; Sec. 12, T1S, R14W, Hollywood Quadrangle, 7.5-minute Series, U.S. Geological Survey (USGS), 1981.

HORIZON. Upper part of the Puente Formation, late Miocene, upper Mohnian to "Delmontian" Benthic Foraminiferal Stage.

ETYMOLOGY. The specific epithet is in honor of Dr. David P. Whistler, curator emeritus of Vertebrate Paleontology, Natural History Museum of Los Angeles County, for his lifelong endeavors in advancing our knowledge of North American Cenozoic life.

DISCUSSION. *Genyonemus whistleri* shows several features that are diagnostic of the family Sciaenidae, including a long dorsal fin, with a deep notch separating the spinous-rayed and soft-rayed parts; the third element of the anal fin not transformed into a spine; medial elements absent in dorsal and anal fin pterygiophores; and exceptionally large otoliths. The overall otolith morphology (a large, shallow ostium; absence of a rostrum or antirostrum; straight, narrow, horizontal cauda, bent ventrally at its posterior end; and the overall subrectangular shape) is characteristic of the genus *Genyonemus*.

DESCRIPTION. The holotype of *G. whistleri* (Figs. 3–6) is a nearly complete articulated skeleton that lacks the anterodorsal portion of the head and has an incomplete right saccular otolith *in situ*. The specimen consists of right and left counterparts that are preserved in light gray silty clay shale. The following description is mainly taken from the left side, which is the better preserved of the two sides.

The body is moderately elongated, having a greatest body depth of 59.83 mm. The estimated standard length is 191 mm, and the estimated total length is 239 mm (the length of the missing portion of the head is estimated on the basis of complete skeletons of *G. lineatus*). Selected measurements are given in Table 3.

The skull is poorly preserved (Fig. 4), and we were unable to identify some of the individual elements of the cranium. In the suspensorial and opercular regions, only the opercle, endopterygoid, metapterygoid, and quadrate are identifiable. The opercle is not preserved with enough detail for any description; the endopterygoid is thin, narrow, and bow shaped; the metapterygoid is subtriangular; the quadrate is triangular and has a straight posterior margin.

Seven incomplete branchiostegal rays are visible in the hyoid region. The rays increase in size posteriorly, and each curves posteriorly to form a thin, ensiform blade. The three smaller rays taper to a blunt point proximally, whereas each of the four larger ones has a slightly thickened head.

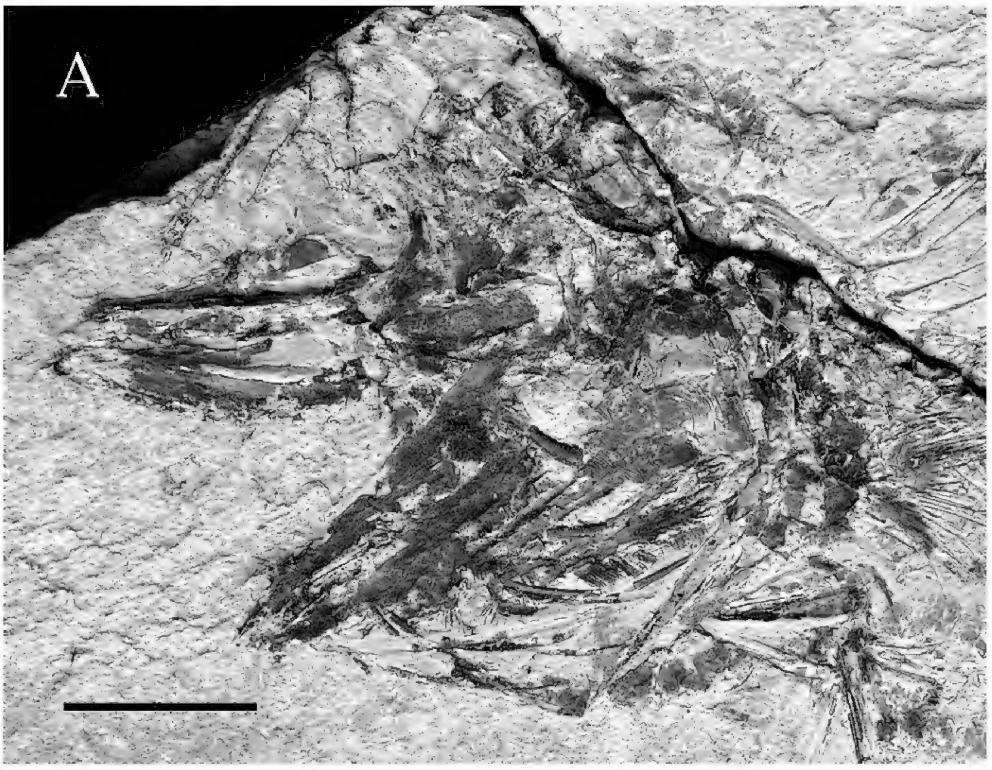
The dentary is long and slender, with a broad band of small, fine, conical teeth on its dorsal surface. The teeth are pointed at their apices. In lateral view, the upper limb of the dentary narrows posteriorly, whereas the lower limb is deep, and its posterior end is vertical. A groove that forms the anterior portion of the preopercu-lomandibular canal of the lateral line system is present along the entire length of the ventral surface of the dentary. Anteriorly, the groove is bridged by narrow struts that form variably-sized foramina. The maxilla and premaxilla are not preserved.

The vertebral column consists of 12 abdominal and 15 caudal vertebrae (including the urostyle). Neural spines are well developed and pointed, except for those on the last two centra. The first neural spine is autogenous with the centrum. The second and third neural spines are widely separated by the insertion of the third predorsal and first proximal pterygiophore. Ten pleural ribs, slender and tapering posteriorly, articulate with each side of the abdominal vertebrae. The first two abdominal vertebrae lack ribs, whereas each of the remaining abdominal vertebrae bears a rib. The caudal vertebrae have much greater structural uniformity in their lengths than the abdominal vertebrae, except for the last two, which are considerably shortened.

The lunate caudal fin has 17 principal, and 15 branched rays (formula I, 8, 7, I). The procurrent rays overlap each other; thus, we could not make an accurate count. A well-developed procurrent spur (see Johnson, 1975) is present. The caudal skeleton (Fig. 5) contains five unfused hypurals. Three epurals are between the first uroneural and neural spine of the second preural centrum. There are two uroneurals and a urostyle. The parhypural is broad, with a distinct parhypurapophysis.

An almost complete dorsal fin skeleton is preserved. Three predorsals are between the skull and first pterygiophore. The first predorsal extends in front of the first neural spine, the second and third predorsals interdigitate between the first and second and the second and third neural spines, respectively. The first dorsal fin contains 11 spines, and the second dorsal fin contains one spine and 24 soft rays. The spines are grooved lengthwise along their posterior surfaces, and the soft rays are segmented and branched. The dorsal fin is supported by 36 proximal pterygiophores, the first supporting the first two spines. The proximal pterygiophores are bisegmental, and a well-ossified stay is present.

The anal fin has its origin slightly posterior relative to the insertion of the first dorsal fin. Two spines and 11 soft rays are in the anal fin, and both spines articulate with the first proximal pterygiophore. The first anal spine is more slender and shorter than the second anal spine, and the soft rays are segmented and branched. We were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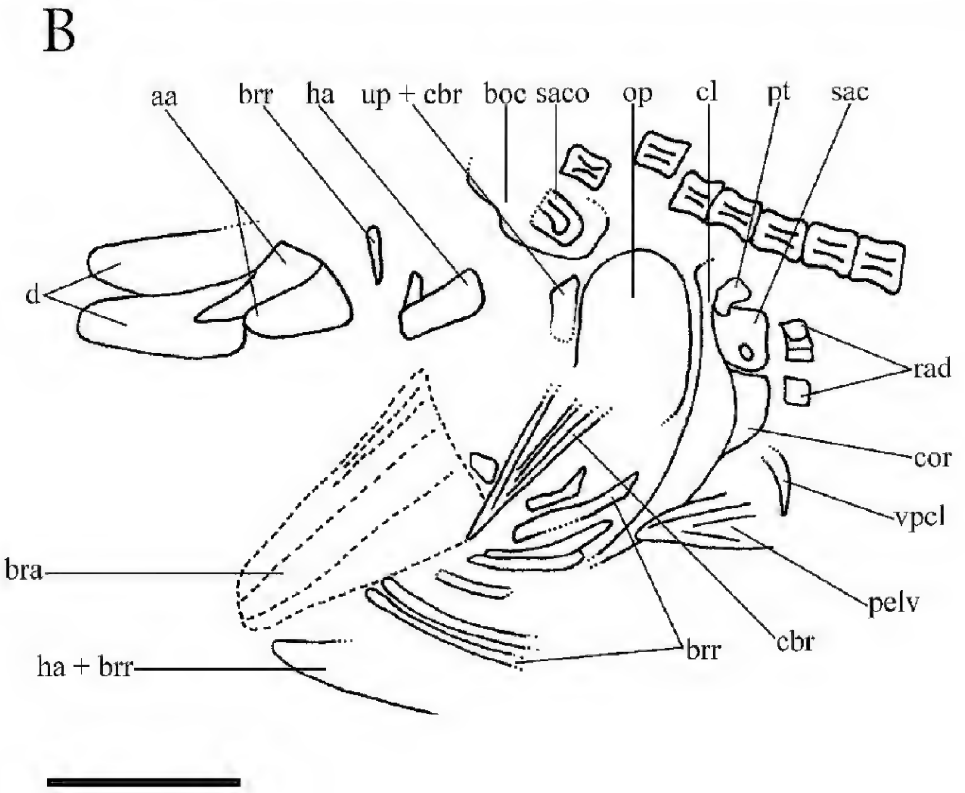
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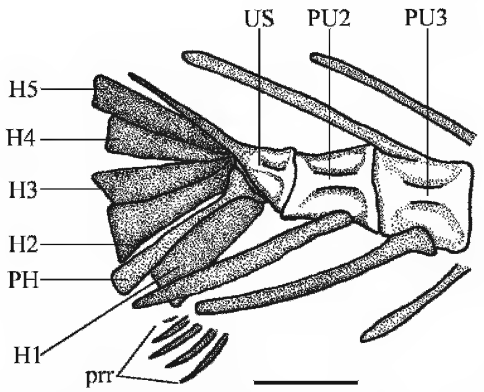

Figure 5 *Genyonemus whistleri* sp. nov., line drawing of the caudal skeleton. **ABBREVIATIONS: H1–5** = hypural 1–5; **PH** = parhypural; **prr** = procurrent ray; **PU2–3** = preural centrum; **US** = urostyle. Scale bar = 2 cm.

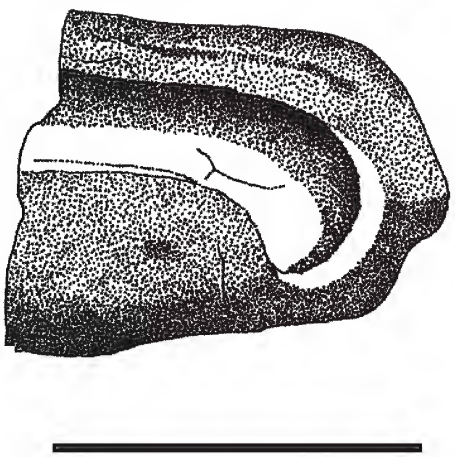

Figure 6 *Genyonemus whistleri* sp. nov., drawing of incomplete right saccular otolith of holotype, LACM 144152. Scale bar = 5 mm.

unable to accurately count the number of proximal pterygiophores because they overlap each other.

The pectoral fin is composed of at least 19 rays. The pectoral fin rays are short and do not reach beyond the anal fin origin. There are four hourglass-shaped radials. The scapula is roughly rectangular, except that the posterodorsal corner is concave. The scapular foramen is moderate in size. The coracoid is V-shaped and its ventral arm gradually tapers to a point. The cleithrum consists of a short dorsal limb and forms an angle of approximately 120 degrees with the longer ventral limb.

Each pelvic fin is composed of one spine and five soft branched rays. The well-preserved basipterygia are thin and triangular and have keels and processes.

Ctenoid scales cover the entire body and extend onto the caudal fin. The lateral midbody scales are large and rectangular, and their anterior–posterior length ranges from 5.36 to 5.49 mm, and the dorsal–ventral height ranges from 4.36 to 5.02 mm. The scales have eight to 11 anterior (basal) radii and a focus positioned posterior to the center of the scale.

The inner face of the left otolith is missing, and all of the diagnostic features are absent. The right otolith is preserved so that its diagnostic inner face is exposed (Fig. 6). Approximately one-third of its anterior end is missing, but the impression of the missing anterior fragment indicates an estimated total length of 8.29 mm, and its greatest height is 4.37 mm. The preserved posterior section measures 5.43 mm. The preserved inner face is relatively flat, or slightly convex and subrectangular in shape with a relatively flat outer face, and no umbo can be detected. Impression of the anterior otolith indicates that the anterior end might have been sharply rounded and bullet shaped. The dorsal rim is nearly flat with the posterodorsal margin rounded, and the ventral rim expanding anteriorly with the posteroventral area indented and curved inwardly. The cauda is narrow with its anterior long and horizontal and its posterior short and sharply bent ventrally.

DISCUSSION

THE FOSSIL RECORD OF *GENYONEMUS*

Before this report, the genus *Genyonemus* included one extant species, *G. lineatus*, and one fossil species, *Genyonemus calvertensis* Müller, 1999. The extant species *G. lineatus* is found from southern Baja California northward to Vancouver Island, British Columbia, and it is most abundant from Southern California northward to around Monterey (Skogsberg, 1939; Miller and Lea, 1972; Hart, 1973). These are bottom-dwelling fishes, found schooling and feeding in

←

Figure 4 *Genyonemus whistleri* sp. nov., skull of holotype, LACM 144152, right counterpart: **A**, photograph; **B**, line drawing of A. **ABBREVIATIONS: aa** = anguloarticular; **boc** = basioccipital; **bra** = branchial arches; **brr** = branchiostegal rays; **cbr** = ceratobranchials; **cl** = cleithrum; **cor** = coracoid; **d** = dentary; **ha** = hyoid arch; **op** = opercular; **pelv** = pelvic bone; **pt** = posttemporal; **rad** = radials; **sac** = scapula; **saco** = saccular otolith; **up** = upper pharyngeal tooth plate; **vpcl** = ventral postcleithrum. Scale bars = 2 cm.

Table 1 Comparison of some meristic features between *Genyonemus whistleri* sp. nov., Recent *Genyonemus lineatus*, and other California fossil sciaenids. Data from Jordan (1921), David (1943), Miller and Lea (1972), and personal observation.

	Dorsal fin rays	Anal fin rays	Total vertebrae	Caudal vertebrae
Genyonemus whistleri sp. nov.				
Holotype (LACM 144152)	XI + I, 24	II, 11	27	15
Genyonemus lineatus	XII–XV + I, 18–25	II, 10–12	26	15
Lompoquia culveri	XI + I, 11	II, 9–12	26	14
Lompoquia retropes	X + I, 12–14	II, 10–12	26–27	14
Cynoscion (Aristoscion) eprepes	XI + I, 20	II, 12–14	24–25	10–11

warm, shallow, nearshore waters. They are usually found in loose schools over sand or mud substrates in bays and estuaries and in water less than 30 m deep just outside the surf zone (Chao, 1995). *Genyonemus lineatus* can reach 380 mm in length and weigh over 0.5 kg (Chao, 1995).

Previously known fossil occurrences of *Genyonemus* were based solely on the otolith record from the east and west coasts of North America and South America, with a known geochronologic range from Miocene to Pleistocene. *Genyonemus whistleri* is the first fossil representative of the genus to be based on skeletal material. The earliest known occurrence of the genus, *G. calvertensis* is reported from the early to middle Miocene (17.5–14.5 Ma) Plum Point Marl Member of the Calvert Formation, Prince George County, Maryland (Müller, 1999:184, figs. 38/1–4).

The only *Genyonemus* remains known thus far from South America are otoliths that have been attributed to *Genyonemus* sp. from the late Pliocene Canoa Formation of western Ecuador (Landini et al., 2002:30, table 1). This represents the southernmost occurrence of the genus. The material was not described or figured, but the *Genyonemus* otoliths consist of well-preserved specimens (G. Carnevale, personal communication, 2006).

Fossil otoliths of the Recent species, *G. lineatus*, are commonly found in Pliocene and Pleistocene sediments of California (Kanakoff, 1956; Fitch, 1964, 1966, 1967, 1968, 1970). The earliest occurrence of *G. lineatus* is from the late Pliocene Fernando Formation of Southern California (Fitch and Reimer, 1967). *Genyonemus lineatus* has also been reported from Southern California in the late Pleistocene Palos Verdes Sand, from the underlying Pleistocene San Pedro Sand (Kanakoff, 1956; Fitch, 1964, 1966, 1967, 1970), and from the early Pleistocene Timms Point Silt (Fitch, 1968).

Fitch (1970) also reported *G. lineatus* from Pleistocene deposits (LACM locality 3246) north of Arcata, in northern California, and this marks the northernmost occurrence of *G. lineatus* in the fossil record. The age of the latter deposits is in dispute, although Fitch (1970) interpreted these Pleistocene deposits as being age-equivalent to the Palos Verdes Sand in Southern California. Surficial geologic mapping compiled by Strand (1963) placed the locality in the Pleistocene marine and terrace deposits of the Battery Formation. Maxson

Table 2 Comparison of proportional ratios for saccular otoliths between the species of *Genyonemus*. **ABBREVIATIONS:** **H** = otolith height; **L** = otolith length; **T** = otolith thickness; **cl** = caudal length; **n** = number; **oh** = ostium height; **ol** = ostium length; **SL** = standard length; **x** = horizontal portion of cauda; **y** = down-turned portion of cauda; **x:y** = caudal curvature index (cci); **SD** = standard deviation; **CV** = coefficient of variation. See "Methods and Materials" section and Figure 2 caption for definition of abbreviations.

	L:H	H:T	cl:ol	ol:oh	x:y	SL:L
Genyonemus whistleri, sp. nov.						
Holotype (LACM 144152)	1.90	—	—	—	2.38	23.04
Genyonemus calvertensis						
Paratype [388(P15)]	1.74	2.20	0.97	1.87	3.46	—
Genyonemus lineatus						
Mean	1.97	1.84	0.87	1.61	2.51	16.51
SD	0.13	0.19	0.06	0.12	0.46	1.88
CV	6.51	10.12	7.18	7.24	18.42	11.20
Maximum	2.27	2.20	1.00	1.97	3.67	20.71
Minimum	1.77	1.5	0.75	1.41	1.64	13.36
n = 50						

Table 3 Selected counts and measurements for the holotype of *Genyonemus whistleri* sp. nov. Counts indicated by an asterisk (*); roman numbers correspond to fin spines.

	Measurements (mm)/counts
Total length	239
Standard length	191
Head length	74
Predorsal length	91
Preanal length	143
Head depth	67
Body depth	60
Caudal peduncle depth	18
Dorsal fin	XI + I, 24*
Anal fin	II + 11*
Pectoral rays	≥19*
Pelvic rays	I + 5*
Principal caudal fin	17*
Vertebrae (total)	27*
Vertebrae (abdominal)	12*
Vertebrae (caudal)	15*

(1933) and Back (1957) concluded that the Battery Formation is Pleistocene in age on the basis of an invertebrate fauna, but Moore and Silver (1968) believed that this formation dates from the most recent Pleistocene interglaciation, Sangamon (125,000–75,000 BP). Thus, it is unlikely that these deposits are equivalent to the Palos Verdes Sand, as was interpreted by Fitch (1970).

Other reported fossil material that might belong to *Genyonemus* includes the following. Müller (1999:184–185, figs. 38/5–6) in his extensive monograph of the Tertiary bony fish fauna of the U.S. Atlantic Coastal Plain, described "genus aff. *Genyonemus*" *pertenuis* on the basis of two saccular otoliths from the early to middle Miocene Plum Point Marl Member of the Calvert Formation in Prince George County, Maryland. Müller (1999) considered the fossil species to be related to *Genyonemus*, but the otolith is much thinner and more elongated than others that have been assigned to the genus. He noted that the morphological differences in the otolith exceed the range of variation found in *Genyonemus* otoliths and concluded that the species likely belongs to an undescribed extinct genus. After reviewing the type material of this species, D. Nolf (personal communication, 2006) concluded that the specimens are referable to *Genyonemus*, so further study is needed.

DEPOSITIONAL ENVIRONMENT

The geology at the Vermont/Sunset Station locality, the type locality of *G. whistleri,* is consistent with the continental margin of a deep-water open marine environment off the Miocene coast of California (Dibblee, 1989). Rhythmically alternating graded sandstones and shales represent submarine fans and fan deltas along the continental shelf margin. The strata consist of fine sand, silt, and clay that suggest deposition at the distal end of a fan. The deposits are interpreted as episodes of mass-gravity transport of sediments from a continental source area into a deep-water marine environment

Table 4 Late Miocene paleoichthyofauna at LACM locality 6948, Sunset/Vermont Station, Hollywood District, Los Angeles, California.

Osteichthyes	
Clupeidae	*Ganolytes cameo* Jordan (in Jordan and Gilbert, 1919)
	Ganolytes sp.
	Xyne grex Jordan and Gilbert, 1919
Argentinidae	*Argentina* sp.
Microstomatidae	Genus and species not determined
Alepocephalidae	Genus and species not determined
Gonostomatidae	*Cyclothone* sp.
Sternoptychidae	*Argyropelecus* sp.
Stomiidae	*Chauliodus eximius* Jordan and Gilbert (in Jordan, 1925)
Neoscopelidae	?*Scopelegys* sp.
Myctophidae	Genus and species not determined
Moridae	Genus and species not determined
Melamphaidae	*Scopelogadus* sp.
Serranidae	*Paralabrax* sp.
Carangidae	*Decapterus* sp.
Sparidae	?*Plectrites classeni* Jordan (in Jordan and Gilbert, 1920)
Sciaenidae	*Genyonemus whistleri* sp. nov. (this paper)
	Lompoquia sp.
Zaphlegidae	*Thyrsocles* sp.
Scombridae	*Sarda* sp.
	Scomber sp.

(Lamar, 1970; Critelli et al., 1995). These alternate with sequences of shale that reflect normal deposition from suspension settling. Benthic foraminifera recovered at the locality are interpreted to represent a depth from 400 to 1,400 m (Boettcher and Kling, 1993). This result is similar to other microfossil samples taken from the downtown Los Angeles area and reported by Natland (1957) and Lamar (1970).

The fish fossils found at the site support the reconstruction of the paleoenvironment of the Vermont/Sunset Station locality. The ichthyofauna is represented by 230 specimens that belong to at least 17 families (Table 4). On the basis of the depth preferences of the closest related living taxa, mesopelagic, epipelagic, and a few nearshore forms are represented. The fauna is dominated by the presence of members of the families Alepocephalidae (slickheads), Gonostomatidae (bristlemouths), Microstomatidae (pencilsmelts), Moridae (deepsea cods), Myctophidae (lanternfishes), Neoscopelidae (blackchins), Sternoptychidae (marine hatchetfishes), and Stomiidae (barbeled dragonfishes), all indicating a deep-water, marine, lower mesopelagic environment. The Myctophidae are by far the most abundant fishes in the examined material, with 135 recognizable specimens (88 skeletons and 47 isolated otoliths). The Gonostomatidae, Microstomatidae, and Moridae are also well represented in the assemblage, with more than 17 specimens each. The Alepocephalidae are less common, with five specimens, whereas representatives of the other families (Neoscopelidae, Sternoptychidae, and Stomiidae) are each restricted to a single specimen. All fossil fish from the locality are confined to the thin laminated shale layer, indicating that the epipelagic forms were not transported offshore from a nearshore environment. It is probable that the presence of the epipelagic families Clupeidae (herrings) and Scombridae (mackerels and tunas) results from postmortem transport from higher in the water column. These fishes are considered to have been living in the water column, thus the actual depth of the depositional environment is greater than the depth range of the taxa contained within it. The nearshore components of the fauna (Sciaenidae [croakers and drums], Serranidae [sea basses], and Sparidae [porgies]) are likely the result of postmortem transport from a nearshore environment. The presence of deep-water marine species, and their dominance of the ichthyofauna, combined with the geologic and microfossil data, indicates that the Vermont/Sunset Station locality represents a deep-water marine, lower mesopelagic environment.

OTOLITHS *IN SITU*

Otoliths are calcareous structures associated with the ear in teleost fishes, and they are thought to be involved in both auditory and vestibular functions (Popper and Fay, 1993). They comprise three calcium carbonate structures formed in labyrinths of the neurocranium, mainly of aragonite and organic matter called otoline (Nolf, 1985). Otoliths are common fossils in a wide spectrum of marine sedimentary environments, representing a common way in which fossil teleost fishes are recognized (Nolf, 1995). Patterson (1993), in a survey of the fossil record of teleostean fishes, showed that among the 244 extant families that do have a fossil record, 58 families (24%) are known exclusively from otoliths. In addition, the fossil record for many families is extended considerably geographically and temporally by their otolith fossil records (Nolf, 1995).

On the other hand, complete skeletons of fossil teleost fishes are found in a restricted spectrum of sedimentary environments (e.g., laminated limestones, diatomites, etc.) and represent unusual environmental circumstances (Nolf, 1985, 1995). In these environments, the aragonitic otoliths, which are a metastable polymorph of calcium carbonate, are mostly destroyed and dissolved by diagenetic processes that frequently affect sediments. However, in several Tertiary fossiliferous sites in Europe and North America, skeletons have been found with the otoliths preserved *in situ* (e.g., Gaudant and Reichenbacher, 1998, 2005; Brzobohaty et al., 2003; Huddleston and Takeuchi, 2006). This is an exceptionally rare phenomenon. Nolf (1985:33), in his review of fossil and Recent otoliths, provided a list of only 45 fossil fish species in which otoliths have been noted *in situ* with skeletal remains. In 23 of the 45 species listed, the otoliths are preserved well enough to be taxonomically useful.

A unique quality of the ichthyofauna at the Vermont/Sunset Station locality is that many of the articulated specimens retain their otoliths *in situ*. In addition to the specimen that is described here, five of the 17 families of teleosts at this site (Table 4) are represented by one or more skeletons with otoliths *in situ*, including Melamphaidae (bigscale fishes), Moridae (deepsea cods), Myctophidae (lanternfishes), Neoscopelidae (blackchins), and Serranidae (sea basses). Forty-four of the 88 Myctophidae skeletons retain otoliths *in situ*, and in 14 of the skeletons, the otoliths are preserved well enough to be taxonomically useful. Other localities in the Los Angeles Basin containing this association include an undescribed late Miocene fauna from the Yorba Member of the Puente Formation (LACM locality 6907) in the western Puente Hills (Fitch, 1969; Huddleston and Takeuchi, 2006) and unreported late Miocene sites in the Chino Hills that are also from the Yorba Member of the Puente Formation (LACM localities 6307–6336). These associations form a basis for clarifying

identifications and taxonomic relationships between specimens without preserved otoliths and those that are represented solely by isolated otoliths. Both isolated otoliths and articulated remains should be used to present a more complete record of the Cenozoic ichthyofauna of California.

CONCLUSIONS

1. *Genyonemus whistleri* sp. nov. is a late Miocene sciaenid fish, known only by the holotypic specimen from the upper part of the Puente Formation in the northern Los Angeles Basin, Hollywood District, Los Angeles, Los Angeles County, California.
2. *Genyonemus whistleri* is the first fossil representative of the genus *Genyonemus* to be based on skeletal material. Before this report, the fossil record of *Genyonemus* was based entirely on the otolith record.
3. The preservation of otoliths *in situ* with articulated fossil fish skeletons is a rare occurrence. These occurrences provide opportunities for clarifying the relationship among taxa represented solely by articulated skeletal material and those represented only by isolated otoliths.
4. The type locality of *G. whistleri* is one of several known sites in the Los Angeles Basin that contain articulated fossil teleost fishes that retain their otoliths *in situ*. All of these localities are restricted to the late Miocene Puente Formation in the northern and eastern Los Angeles Basin.
5. An associated paleoichthyofauna from the type locality of *G. whistleri* indicates a deep-water marine, lower mesopelgic environment and is the most extensive deep-water fossil fish fauna that has been reported from the northern Los Angeles Basin. The presence of the holotype of *G. whistleri* in this deep-water deposit is attributed to postmortem transport from a nearshore environment.

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Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the Central Florida Phosphate District

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ABSTRACT. Forty-seven species of land mammals are present in the latest Hemphillian (early Pliocene) Palmetto Fauna of Florida. This composite fauna comes from fluvioestuarine sediments of the upper Bone Valley Formation exposed in diverse mines within the Central Florida Phosphate District. The fauna, including 18 carnivorans and 22 ungulates, lived at a time of high sea level when the Florida peninsula was only about 5% of its present land area. The ungulate fauna includes a broad array of browsing, mixed-feeding, and grazing species, which is reminiscent of diverse faunas that lived in the Great Plains during the Clarendonian, about 5 million years earlier. About half of the species in the Palmetto Fauna also occur in late Hemphillian faunas of Mexico and the western United States. On the other hand, 12 species appear to be southeastern endemics. A few mammals included in the Palmetto Fauna (or Upper Bone Valley Fauna) in previous studies, including mylodontid and megatheriid ground sloths, *Epicyon*, *Leptarctus*, *Aphelops*, *Hipparion*, and *Calippus*, are excluded because of a lack of *in situ* representatives in early Pliocene strata and/or corrected identifications.

INTRODUCTION

Beginning more than a century ago, open-pit phosphate mining operations in south-central Florida produced so many fossil vertebrates that the source sediments were named the Bone Valley Gravel by Matson and Clapp (1909), a stratigraphic unit later called the Bone Valley Formation (e.g., Cooke, 1945). For many years, the fossils were assumed to be a chronologically unified fauna (Sellards 1915a, 1916; Simpson 1930; Olsen, 1959). In the past several decades, however, field parties of the Florida Museum of Natural History (FLMNH) have augmented the faunal diversity and elucidated the stratigraphic complexity of the Bone Valley faunal succession. In this contribution, we summarize the current status of the terrestrial mammals from the uppermost (and richest) faunal horizon of the Bone Valley Formation, the Palmetto Fauna.

Webb and Hulbert (1986) proposed formal names for the three most commonly found mammalian assemblages from the Bone Valley Formation: the late Barstovian Bradley Fauna; the early Clarendonian Agricola Fauna; and the latest Hemphillian Palmetto Fauna. A rarer, fourth assemblage, the early Hemphillian Four Corners Fauna, was recognized by Hulbert et al. (2003). As documented here, most, but not all, of the terrestrial fossils of the classic "Bone Valley Fauna" of Sellards (1916) and Simpson (1930) belong to the Palmetto Fauna. Beginning in the 1960s, substantial new collections of specimens from the upper Bone Valley Formation resulted from the fieldwork of S. David Webb and collaborators and from generous donations by amateur collectors. These triggered a number of studies on separate components of the fauna (e.g., Webb, 1969, 1973, 1981, 2000; MacFadden and Galiano, 1981; Berta and Galiano, 1983; Wright and Webb, 1984). However, no comprehensive review of the land mammal fauna of the upper Bone Valley has appeared since Simpson (1930).

The Palmetto Fauna is a composite vertebrate assemblage derived from an area of several hundred square kilometers that is sometimes informally referred to as the "Bone Valley," but which is more properly called the Central Florida Phosphate District (CFPD). The fossils occur within a stratigraphic interval of about 10 m in the upper Bone Valley Formation (Morgan, 1994). The richest samples of the Palmetto Fauna were found in the southwest corner of Polk County and the northwest corner of Hardee County, south of the towns of Brewster and Fort Meade, north of the town of Fort Green, and west of the Peace River, at about 27°40′N, 82°00′W. From a paleontological viewpoint, the most productive phosphate mines in this area are the Palmetto, Fort Green, Payne Creek, Gardinier Ft.

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Table 1 Terrestrial mammals from the latest Hemphillian (early Pliocene) Palmetto Fauna, upper Bone Valley Formation, south-central Florida. To the right of the name of each taxon is a numeral indicating the criterion by which it is included in the Palmetto Fauna: 1, specimens collected *in situ* from the upper Bone Valley Formation; 2, no *in situ* specimens, but chronologic range of taxon limited to late Hemphillian; 3, no *in situ* specimens, but mostly found in mines or specific regions in mines that primarily produce other Palmetto Fauna taxa. The otter *Enhydritherium terraenovae* was originally thought to be restricted to shallow marine habitats (Berta and Morgan, 1985), and it was therefore included in Morgan's (1994) list of marine mammals of the Palmetto Fauna. However, this species is now known also to occur in freshwater habitats (Lambert, 1997), so is included here. Apparent southeastern endemics are indicated by an asterisk (*) in the right column.

Xenarthra		
	Megalonychidae	
	Megalonyx curvidens Matthew, 1924	1
Lipotyphla		
	Talpidae	
	gen. et sp. indet.	3
Rodentia		
	Sciuridae	
	Miopetaurista webbi (Robertson, 1976)	1*
	Castoridae	
	Dipoides sp.	3
	Muridae	
	gen. et sp. indet.	1
Lagomorpha		
	Leporidae	
	Hypolagus ringoldensis (Gustafson, 1978)	3
	Nekrolagus progressus (Hibbard, 1939)	3
Carnivora		
	Canidae	
	Borophagus hilli (Johnston, 1939)	1
	Borophagus pugnator (Cook, 1922)	1
	Carpocyon limosus Webb, 1969	3
	Eucyon davisi (Merriam, 1911)	2
	Vulpes stenognathus Savage, 1941	1
	Ursidae	
	Agriotherium schneideri Sellards, 1916	1
	Plionarctos sp.	1
	Procyonidae	
	Arctonasua eurybates Baskin, 1982	1*
	cf. *Nasua* sp.	3
	cf. *Procyon* sp.	1
	Mustelidae	
	Enhydritherium terraenovae Berta and Morgan, 1985	1*
	Plesiogulo marshalli (Martin, 1928)	2
	cf. *Martinogale* sp.	1
	Mephitinae, gen. et sp. indet.	1
	Felidae	
	Lynx rexroadensis (Stephens, 1959)	1
	cf. *Pseudaelurus* sp.	1
	Machairodontinae, gen. et sp. indet.	1
	Machairodus cf. *M. coloradensis* Cook, 1922	1
Proboscidea		
	Mammutidae	
	Mammut matthewi (Osborn, 1921)	1
	Gomphotheriidae	
	Gomphotherium simplicidens (Osborn, 1923)	1*
	Rhynchotherium edense (Frick, 1921)	1
Perissodactyla		
	Tapiridae	
	Tapirus polkensis (Olsen, 1960)	1*
	Tapirus sp. nov.	1
	Rhinocerotidae	

Table 1 Continued.

	Teleoceras hicksi Cook, 1927	1
	Equidae	
	Astrohippus stockii Lance, 1950	2
	"*Dinohippus*" *mexicanus* (Lance, 1950)	1
	Neohipparion eurystyle (Cope, 1893)	1
	Pseudhipparion simpsoni Webb and Hulbert, 1986	1*
	Cormohipparion emsliei Hulbert, 1988	1*
	Nannippus aztecus Mooser, 1968	1
Artiodactyla		
	Tayassuidae	
	Catagonus brachydontus (Dalquest and Mooser, 1980)	1
	Mylohyus elmorei (White, 1942)	1*
	Protoceratidae	
	Kyptoceras amatorum Webb, 1981	1*
	Camelidae	
	Hemiauchenia edensis (Frick, 1921)	1
	Pleiolama vera (Matthew, 1909)	1
	Megatylopus gigas Matthew and Cook, 1909	1
	Gelocidae	
	Pseudoceras sp.	1
	Cervidae	
	Eocoileus gentryorum Webb, 2000	1*
	Antilocapridae	
	Hexameryx simpsoni White, 1941	1*
	Subantilocapra garciae Webb, 1973	1*

Meade, Rockland, and Brewster. For location maps of specific mines, refer to Webb (1981), Wright and Webb (1984), MacFadden (1986), and Morgan (1994). In this area, the lower Bone Valley Formation is generally thin or missing. Both north and south of this region, on the other hand, middle Miocene (Barstovian and Clarendonian) vertebrates become more common. Most mines in the entire CFPD, however, include some deposits of the upper Bone Valley Formation and produce components of the Palmetto Fauna.

In addition to terrestrial mammals, the Palmetto Fauna also includes diverse assemblages of sharks and rays; teleost fish; marine, freshwater, and terrestrial reptiles (e.g., Sellards, 1915b; Dodd and Morgan, 1992); birds (e.g., Wetmore, 1943; Brodkorb, 1955; Becker, 1987); and marine mammals (e.g., Allen, 1941; Domning, 1988; Morgan, 1994). In this study, we only cover the terrestrial mammals, for which a minimum of 47 terrestrial mammalian species are recognized (Table 1). Taphonomic factors produce a significant bias against small-bodied terrestrial vertebrates in the Palmetto Fauna, and screen-washing of large volumes of upper Bone Valley sediment did not produced many small terrestrial mammals. We also compiled a list of terrestrial mammals (Table 2) that are not members of the Palmetto Fauna, contrary to earlier assignments to that fauna *per se*, to the "Upper Bone Valley" Fauna, or to the classic Bone Valley Fauna of Sellards (1916) and Simpson (1930).

METHODS AND MATERIALS

This study is based primarily on specimens housed in the vertebrate paleontology collections of the FLMNH, which contains the largest collection of CFPD vertebrate fossils. Smaller collections are housed in the American Museum of Natural History (AMNH); the Museum of Comparative Zoology, Harvard University (MCZ); the National Museum of Natural History, Smithsonian Institution (USNM); and other institutions and private collections. For the sake of comparability and consistency, our quantitative analyses include only specimens in the FLMNH collections, either in its primary collection (acronym UF) or in the collection formerly housed by the Florida Geological Survey (UF/FGS). Specimens from other collections are included in our analyses only if casts are deposited in either the UF or UF/FGS collections.

Most vertebrate fossils from mines in the CFPD have been and continue to be collected out of stratigraphic context from spoil piles of sediment created by large draglines. The UF collection is unique in containing over a thousand specimens collected directly (*in situ*) from the upper Bone Valley Formation, and it is these specimens that allow us to characterize most of the Palmetto Fauna. At three locations, *in situ* vertebrate fossils occurred in sufficient concentration to permit quarrying: the Whidden Creek Local Fauna from the Gardinier Ft. Meade Mine; the TRO Quarry

Table 2 Disposition of terrestrial mammals placed by early authors such as Simpson (1930) in the Bone Valley Fauna or by later authors in the Upper Bone Valley Fauna (= Palmetto Fauna of this work) either for which there are no specimens with stratigraphic provenance to support their inclusion in the Palmetto Fauna and are probably not late Hemphillian in age or which were misidentified by the indicated author(s).

Taxon	Reference	Current Resolution
Thinobadistes sp.	Webb (1989)	Specimens are early Hemphillian
Megatherium hudsoni	White (1941b)	Pleistocene *Eremotherium*
Epicyon haydeni	Wang et al. (1999)	Specimens are early Hemphillian
Leptarctus progressus	Simpson (1930)	Specimens are middle Miocene, most likely late Barstovian
Aphelops longipes	Simpson (1930)	Specimens are middle Miocene, Barstovian or Clarendonian
Aphelops sp.	Olsen (1957); MacFadden (1998a)	Specimens are middle Miocene, Barstovian or Clarendonian
Calippus sp.	MacFadden (1998b)	Specimens are middle or late Miocene
Hipparion ingenuum	Sellards (1916); Simpson (1930)	Referred Bone Valley specimens are either *Nannippus aztecus* or *Cormohipparion emsliei*
Nannippus ingenuus	MacFadden (1998b)	Bone Valley specimens are Clarendonian or early Hemphillian
Hipparion plicatile	Sellards (1916); Simpson (1930)	Referred Bone Valley specimens are *C. emsliei*
Cormohipparion plicatile	MacFadden (1998b)	Bone Valley specimens are Clarendonian or early Hemphillian
Serridentinus floridanus	Simpson (1930)	Bone Valley specimens are *Rhynchotherium edense*
Procamelus minor	Sellards (1916)	Referred specimen is middle or late Miocene (it is not *Hemiauchenia edensis*)
Procamelus sp.	Olsen (1957)	Either refers to specimens of *Pleiolama vera* or to those of Miocene age

in the Payne Creek Mine; and the Palmetto Microsite in the Palmetto Mine. Many other *in situ* finds were acquired by surface prospecting the ephemeral exposures of open mine faces.

We accept mammals as members of the Palmetto Fauna on the basis of three criteria, each with a different degree of certainty. The status of each species, with respect to these criteria, is indicated in Table 1. First, taxa represented by specimens with species-level diagnostic characters collected *in situ* from the upper Bone Valley Formation are considered members of the Palmetto Fauna without reservation, unless there is clear preservational evidence of reworking. Of the 47 terrestrial mammals currently placed in the Palmetto Fauna, 38 meet this criterion. Second, species from the Bone Valley Formation whose chronologic ranges are limited to the late Hemphillian, on the basis of evidence outside of Florida, are considered to be members of the Palmetto Fauna even if no known CFPD specimens have been collected *in situ*. Three rare species are placed in the Palmetto Fauna by this criterion. Third, species that were not collected in place, but which came recurrently from mines that regularly sample the Palmetto Fauna, are provisionally assigned to that fauna. This third criterion applies to the Palmetto, Brewster, Gardinier Ft. Meade, Payne Creek, Fort Green, and Rockland mines and permits us to add six more species to the current faunal list. In contrast, species are excluded from the Palmetto Fauna if they are not known from *in situ* deposits of the upper Bone Valley Formation and are either rare or absent from the mines cited above. The evidence against inclusion in the Palmetto Fauna increases for taxa that are known principally from mines that typically provide thick exposures of the lower Bone Valley Formation and produce abundant middle Miocene vertebrates. These mines include Phosphoria, Hookers Prairie, Silver City, Kingsford, Nichols, and Hardee Complex.

We have not followed Scott (1988) in his inflation of the Peace River Formation to subsume the Bone Valley Formation as a member. Instead, we concur with Morgan (1994) in sustaining the traditional use of the Bone Valley Formation of Matson and Clapp (1909) as a readily recognizable and economically important geological unit. We follow the recent review by Tedford et al. (2004) for the boundaries of the Hemphillian Land Mammal Age and its four subdivisions. In particular, the age of the Palmetto Fauna is latest Hemphillian (Hh4), or about 5 to 4.7 Ma.

SYSTEMATICS

MEGALONYCHIDAE

The megalonychid ground sloth *Megalonyx curvidens* Matthew, 1924, is the lone xenarthran in the Palmetto Fauna. About 70 isolated teeth, cranial fragments, and postcranial elements of *M. curvidens* are known, none of which have been illustrated or cited in the literature. About half the specimens were collected *in situ*, most of them from the Gardinier Ft. Meade and Palmetto

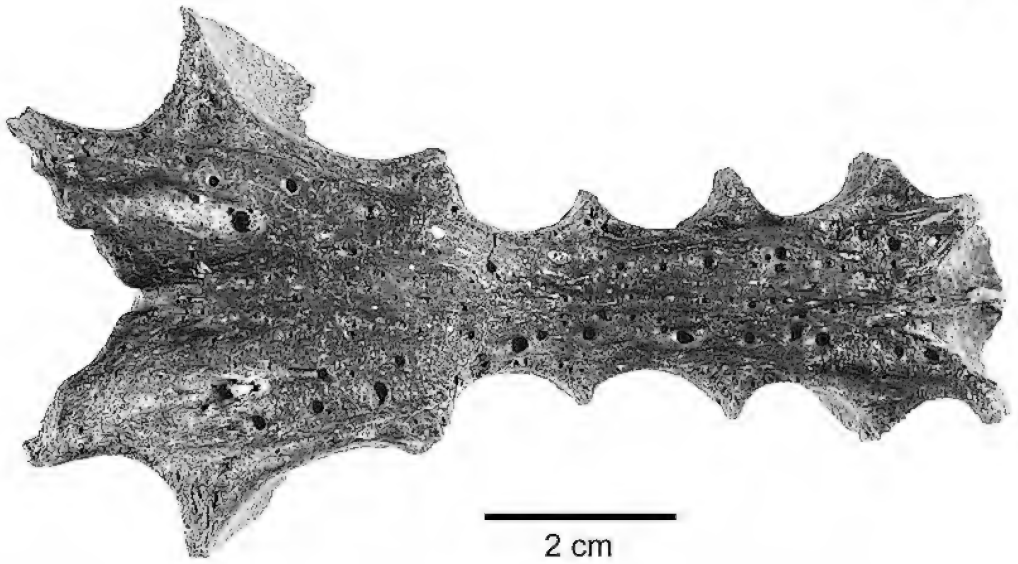

Figure 1 *Megalonyx curvidens* Matthew, 1924, edentulous palate in occlusal view, UF 117668.

mines. The sample from the Whidden Creek Local Fauna includes a palate (UF 117668, Fig. 1), two caniniform (UF 212443–212444) and six molariform teeth (UF 133929–133932, 212445, 212451), two astragali (UF 133933, 212455), a femur (UF 212450), and 17 other postcranial elements.

Megalonyx curvidens is distinguished from the early Hemphillian megalonychid *Pliometanastes protistus* Hirschfeld and Webb, 1968, by its larger size and the shape of its caniniform teeth. Two late Hemphillian species of *Megalonyx* are described: *Megalonyx mathisi* Hirschfeld and Webb, 1968, and *M. curvidens*. Hirschfeld and Webb (1968) based their revised diagnosis and description of *M. curvidens* primarily on a mandible with complete dentition from the late Hemphillian (Hh3) ZX Bar Local Fauna in Nebraska, although the holotype of *M. curvidens*, an isolated lower third molariform tooth, is actually from the slightly older (Hh2) *Aphelops* Draw Fauna, also from Nebraska. The Palmetto Fauna megalonychid teeth are similar in size and morphology to *M. curvidens* and are referred to that species. *Megalonyx mathisi* is known only by an edentulous partial skull from Black Rascal Creek, California (Hirschfeld and Webb, 1968).

TALPIDAE

The order Lipotyphla is represented in the Palmetto Fauna by a single complete humerus (UF 115980) of a mole collected at the Palmetto Microsite. The humerus is longer and more slender than the shorter, robust humerus of *Scalopus aquaticus* (Linnaeus, 1758) that inhabits Florida today. UF 115980 is more similar to the humerus of *Condylura cristata* (Linnaeus, 1758) but needs more comparisons with North American Pliocene moles (Hutchison, 1968).

SCIURIDAE

The second known specimen of the large flying squirrel, *Miopetaurista webbi* (Robertson, 1976) was collected *in situ* from the Gardinier Ft. Meade Mine (Evans, 2000). The holotype of this species, originally placed in the genus *Cryptopterus* Mein, 1970, is from Haile 15A, a late Blancan site in north-central Florida. The new specimen consists of the posterior part of the dentary with slightly worn m2–3 (UF 95701; Fig. 2). The molars are notable for their great complexity, with crenulated ridges and grooves. They are also much larger than other North American flying squirrels: m2 length, 4.5 mm; m2 width, 3.5 mm. The two Florida specimens of *Miopetaurista* are the only records of the genus in North America. This species compares in many

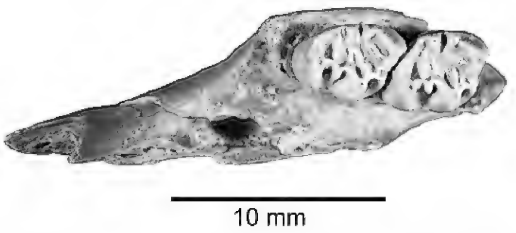

Figure 2 *Miopetaurista webbi* (Robertson, 1976), right dentary with m2 and m3 in occlusal view, UF 95701.

respects with the late Miocene European *Miopetaurista tobieni* (Mein, 1970) and presumably represents a dispersal from Eurasia (Robertson, 1976; Tedford et al., 2004).

CASTORIDAE

Beavers are represented in the Palmetto Fauna by two partial dentaries (UF 21602 and 21603) referred to an undetermined species of *Dipoides* Schlosser, 1902. Both were collected in the Palmetto Mine. *Dipoides* is a widespread genus from the Hemphillian and Blancan in North America (Korth, 1994). The *Dipoides* specimens from the Palmetto Fauna are currently under study by Gary S. Morgan and Richard C. Hulbert, Jr. (R.C.H.), to determine their specific identity.

MURIDAE

The only small rodent cheek teeth (UF 12249–12250) from the Palmetto Fauna were both collected from the Palmetto Microsite. One is a very heavily worn M2, the other a virtually unworn M1. Neither can be assigned to a genus or species at present.

LEPORIDAE

Two rabbits are known from the Palmetto Fauna, the archaeolagine *Hypolagus ringoldensis* (Gustafson, 1978) and the leporine *Nekrolagus progressus* (Hibbard, 1939). White (1987) referred an isolated p3 (UF 95700) from the Gardinier Ft. Meade Mine to *H. ringoldensis*. Elsewhere, *H. ringoldensis* is known from the late Hemphillian of Nebraska and Arizona and the early Blancan of Washington, Kansas, Texas, and Arizona (White, 1987). *Nekrolagus progressus* is represented by a dentary with p3–m3 (UF 12343) from the Palmetto Mine. White (1991:76) mentioned the presence of *N. progressus* from the "Hemphillian of Florida," but he did not cite or illustrate any specimens to document this. From personal communication, we are certain he was referring to UF 12343. All other localities with *N. progressus* are early Blancan in age (White, 1991).

CANIDAE

The most common carnivorans in the Palmetto Fauna are borophagine canids, which compose almost 30% of identifiable carnivoran teeth and jaws. Wang et al. (1999) recognized five borophagines in the Palmetto Fauna: *Borophagus dudleyi* (White, 1941), *Borophagus hilli* (Johnston, 1939), *Borophagus pugnator* (Cook, 1922), *Carpocyon limosus* Webb, 1969, and *Epicyon haydeni* (Leidey, 1858). We reject the occurrence of *E. haydeni* in the Palmetto Fauna (Table 2). All specimens of that species from the CFPD were either collected *in situ* with members of the early Hemphillian Four Corners Fauna (Hulbert et al., 2003) or were collected in areas of mines where that fauna is prevalent. This limits the range of this species in Florida to the late Clarendonian through early Hemphillian, more in line with that observed in the Great Plains (Wang et al., 1999). Only *B. hilli* and *B. pugnator* were collected *in situ* from the upper Bone Valley Formation (Table 1).

Wang et al. (1999) provided detailed descriptions, illustrations, and systematic histories of the two common canids in the Palmetto Fauna *B. pugnator* and the larger *B. hilli*. Wang et al. (1999) retained *B. dudleyi* as a valid species on the basis of the large size and elaborate frontal sinus in the holotype, MCZ 3688, but referred no other specimens to this species. MCZ 3688 is an edentulous partial skull (White, 1941a) that lacks stratigraphic provenance, but it is more similar in size and features of the frontal sinus to Blancan species of *Borophagus* (Wang et al., 1999). However, Blancan faunas are not known from the CFPD (Morgan, 1994). Answers to questions regarding the validity and geologic age of *B. dudleyi* will require additional specimens, preferably collected from *in situ* deposits.

The holotype, and only known CFPD specimen, of *C. limosus* is a partial palate (Webb, 1969). It was collected from a spoil pile from the Palmetto Mine with specimens of *Hexameryx simpsoni* White, 1941, and *Neohipparion eurystyle* (Cope, 1893), both common members of the Palmetto Fauna. The only other specimens of *C. limosus* are from the early Hemphillian Port of Entry Pit in Oklahoma (Wang et al., 1999) and the late Hemphillian Wyman Creek Local Fauna in Nebraska (Tucker, 2003). *Carpocyon* is a hypocarnivorous genus otherwise restricted to the Barstovian and Clarendonian (Wang et al., 1999).

The subfamily Caninae is represented in the Palmetto Fauna by only three identifiable specimens representing two species. *Eucyon davisi* (Merriam, 1911) is known from a dentary (UF 45884; Fig. 3A) and an isolated P4 (UF 58373), both from the Fort Green Mine. Evidence for the fox *Vulpes stenognathus* Savage, 1941, consists only of a partial dentary collected *in situ* from the upper Bone Valley Formation in Nichols Mine (UF 23994; Fig. 3B).

URSIDAE

Two bears occur in the Palmetto Fauna, the huge *Agriotherium schneideri* Sellards, 1916, and a species of the much smaller *Plionarctos* Frick, 1926. Together they make up about 22% of identifiable carnivoran teeth and jaws. Sellards (1916:plate 12) based *A. schneideri* on a right dentary. Fifteen additional specimens of *A.*

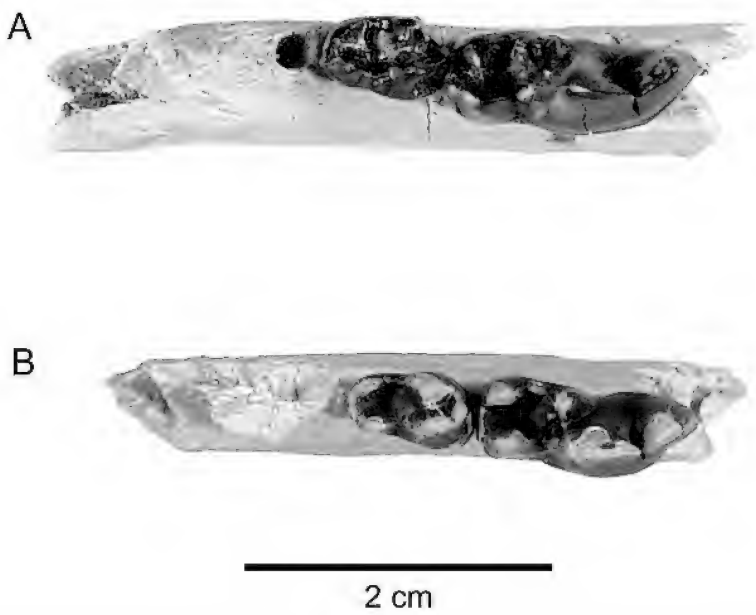

Figure 3 Canids: **A,** *Eucyon davisi* (Merriam, 1911), right dentary with m1 and m2 in occlusal view, UF 45884; **B,** *Vulpes stenognathus* Savage, 1941, right dentary with m1 and m2 in occlusal view, UF 23994.

schneideri from the CFPD, mostly isolated teeth, are in the UF and UF/FGS collections; of these, three were collected *in situ* in the upper Bone Valley Formation. The most significant example is a maxillary fragment with M2 (UF 133944) from the Whidden Creek site. Hunt (1998) regarded *A. schneideri* as the only valid species of *Agriotherium* in North America.

Plionarctos is known from 19 CFPD specimens, including four from the Whidden Creek site. Figure 4A shows UF 40094, a right dentary with m2 and m3. The remaining specimens, although not collected *in situ*, mostly come from regions in the Fort Green, Palmetto, and Gardinier mines that have produced abundant Palmetto Fauna taxa. Two species of *Plionarctos* are

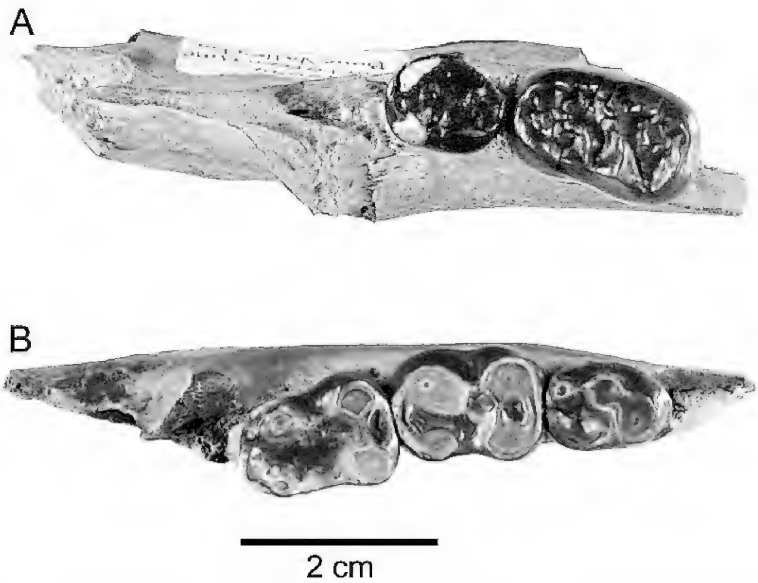

Figure 4 Carnivorans: **A,** *Plionarctos* sp., right dentary with m2 and m3 in occlusal view, UF 40094; **B,** *Arctonasua eurybates* Baskin, 1982, left dentary with p4–m2 in occlusal view, UF 24390.

known, *Plionarctos edensis* Frick, 1926, from the late Hemphillian Mount Eden Fauna, California, and *Plionarctos harroldorum* Tedford and Martin, 2001, from two early Blancan faunas in Washington. The identity of the Palmetto Fauna sample of *Plionarctos* has not yet been determined but is currently under study.

PROCYONIDAE

Three procyonids are present in the Palmetto Fauna, and together they make up about 12% of identifiable carnivoran teeth and jaws. The most common is *Arctonasua eurybates* Baskin, 1982, represented by 10 specimens. A partial dentary with two teeth (UF 24390) was collected *in situ* from the upper Bone Valley Formation in the Palmetto Mine. Figure 4B shows a left dentary with p4–m2 (UF 24389). Two distal humeri from the Whidden Creek site (UF 133941, 133942) are very similar to, but larger than, humeri of *Arctonasua floridana* Baskin, 1982, from the late Clarendonian Love Bone Bed of Florida.

Baskin (1982, 1998) listed two other procyonids from the upper Bone Valley Formation: the extant genera *Nasua* Storr, 1780, and *Procyon* Storr, 1780. Baskin (1982:fig. 12A) identified a partial dentary from the Palmetto Mine (UF 18920) as ?*Nasua*. Three other fragmentary dentaries, UF 53829, 90957, and 212697, apparently represent the same taxon. This is the earliest record of *Nasua* (Baskin, 1998), although because none of the specimens was collected *in situ*, their age is tentative. Baskin (1998) listed *Procyon* sp. from the Palmetto Fauna on the basis of a dentary in the AMNH collection (Baskin, personal communication). The UF collection has five additional specimens of *Procyon* sp., including a dentary with m2 (UF 102071) from Kingsford Mine, an isolated m2 (UF 25923) from the Palmetto Microsite, and a distal humerus from the Whidden Creek site (UF 123831).

MUSTELIDAE

Four species of mustelids occur in the Palmetto Fauna: *Pleisogulo marshalli* (Martin, 1928); *Enhydritherium terraenovae* Berta and Morgan, 1985; and two mephitines, cf. *Martinogale* sp. and an unidentified smaller skunk (Table 1). Together they make up about 17% of identifiable carnivoran teeth and jaws. Harrison (1981:fig. 10e and 10f) described and illustrated the only two specimens of *P. marshalli* from the Palmetto Fauna. Both lack stratigraphic provenance, but *P. marshalli* is considered a member of the Palmetto Fauna because, in North America, it is restricted to the late Hemphillian (Harrison, 1981; Teford et al., 2004).

Berta and Morgan (1985) described the giant otter *E. terraenovae* from the CFPD and referred specimens from Withlacoochee River 4A in north-central Florida and two faunas from Southern California. The UF collection contains about 20 specimens of this species from the CFPD, of which four were collected *in situ* in late Hemphillian deposits: a dentary (UF 125000) and proximal tibia (UF 133943) from the Whidden Creek site; a dentary (UF 68001) from the Gardinier Ft. Meade Mine; and a tibia (UF 40087) from the TRO Quarry. Of the specimens lacking stratigraphic provenance, most derive from the Palmetto, Fort Green, Gardinier Ft. Meade, and Rockland mines. A remarkable specimen of *E. terraenovae*, consisting of a nearly complete articulated skeleton from Moss Acres in north-central Florida (Lambert, 1997), has made it possible to confirm the identification of isolated postcranial elements from the CFPD as *Enhydritherium*. Berta and Morgan (1985) proposed that *Enhydritherium* was a sea otter for morphological reasons and because it was generally restricted to marine vertebrate faunas in Florida and California. However, the presence of *Enhydritherium* in Moss Acres and Withlacoochee River 4A, neither of which contains marine vertebrates, suggests that this taxon also frequented freshwater habitats in Florida.

The scarcity of small mustelids in the CFPD is not surprising considering the general rarity of small-bodied terrestrial vertebrates in the Bone Valley Formation. Four partial dentaries and an isolated m1, representing two size classes of mephitines, are present in the UF collection. One of the larger size class, which is tentatively identified as the Hemphillian skunk *Martinogale* Hall, 1930, comes from the Whidden Creek site (UF 135628). A tiny m1 (UF 13065) was collected *in situ* at the Palmetto Microsite. No detailed studies have been made on these specimens.

FELIDAE

Four species of felids occur in the Palmetto Fauna, and together they make up about 18% of identifiable carnivoran teeth and jaws (Table 1). *Lynx rexroadensis* (Stephens, 1959) is the most common felid, represented by 10 dentaries, two maxillae, and 12 postcranial elements. Of these, six were collected *in situ*, five from the Whidden Creek site (including two dentaries, UF 133936 and 135627) and a proximal humerus from the Palmetto Mine (UF 65597). The Palmetto Fauna sample of *L. rexroadensis* was described by MacFadden and Galiano (1981) and Werdelin (1985). A felid about 20% smaller than *L. rexroadensis* is represented only by a distal humerus (UF 100216) collected *in situ* from the Gardinier Ft. Meade Mine. We very provisionally identify it as cf. *Pseudaelurus* sp. in Table 1, but cranial material is necessary to make a secure identification.

A small (leopard-sized) machairodontine felid is the other common cat in the Palmetto Fauna. It is known by 15 specimens, of which 11 were collected *in situ* from the upper Bone Valley Formation: three metacarpals from the TRO Quarry, a calcaneum from Nichols Mine, and three partial dentaries (UF 124634, 135626, and 212381), a humerus (UF 133938), a distal radius (UF 123836), and two tibiae (UF 133939, 212380) from the Whidden Creek site. Most of these specimens were collected after Berta and Galiano (1983) described this CFPD machairodontine as the oldest known sample of *Megantereon hesperus* (Gazin, 1933). The most important new specimen is UF 124634 because it preserves the entire symphysis and lower canine, which were unavailable to Berta and Galiano. Turner (1987) and Sardella (1998) disputed Berta and Galiano's (1983) identification of this sample, although to our knowledge without ever seeing any of the new referred specimens. Ongoing analysis of the enlarged Palmetto Fauna sample suggests that Turner's (1987) argument is correct. The new material shows that the smaller CFPD machairodontine differs from *Megantereon* Croizet and Jobert, 1828, in lacking a mandibular flange and by having two or three small mental foramina (instead of one large foramen) and a relatively low main cusp on the p4. Moreover, it differs from both *Megantereon* and *Smilodon* Lund, 1842, by having a relatively large lower canine and a short postcanine diastema. Comparisons are currently underway with other smaller machairodontines, such as *Paramachaerodus* Pilgrim, 1913, and *Adelphailurus* Hibbard, 1943.

A much larger machairodontine, *Machairodus* cf. *M. coloradensis* Cook, 1922, is known from the CFPD by just a few isolated teeth and postcranial elements. Three specimens were collected *in situ* from the upper Bone Valley Formation, placing this taxon in the Palmetto Fauna: a p4 from Gardinier Ft. Meade Mine (UF 100218), an astragalus from Nichols Mine (UF 49061), and a proximal femur from Whidden Creek (UF 123838).

MAMMUTIDAE

We recognize three proboscidean genera in the Palmetto Fauna: one mammutid and two gomphotheres. The two best specimens came from smaller scale mining operations early in the last century. Although their stratigraphic provenance might be questioned, we are now able to supplement the early collections with specimens that confirm the occurrence of all three taxa in the Palmetto Fauna. A total of 86 proboscidean cheek teeth and other gnathic elements in the Palmetto Fauna were identified to species. Of these specimens 16% represent *Mammut matthewi* (Osborn, 1921), 72% are *Rhynchotherium edense* (Frick, 1921), and 12% belong to *Gomphotherium simplicidens* (Osborn, 1923).

The most complete mammutid Palmetto Fauna specimen is the mandible designated by Simpson (1930) as the holotype of *Pliomastodon sellardsi* (UF/FGS 3822). We support the proposal of Lambert and Shoshani (1998) that late Neogene mammutids from North America, traditionally assigned to the genus *Pliomastodon* Osborn, 1926, be incorporated within the genus *Mammut* Blumenbach, 1799. These authors did not present species synonymies for pre-Pleistocene *Mammut*, but they did recognize one pre-Blancan species, namely *M. matthewi* (Osborn, 1921). Simpson (1930) noted that his new species was morphologically closest to *M. matthewi*, which at the time was known only from Nebraska. The minor differences between *Mammut sellardsi* and *M. matthewi* are of similar magnitude as those observed between populations of the wide-ranging Pleistocene *Mammut americanum* (Kerr, 1791), so we propose that *M. matthewi* is the senior synonym of *M. sellardsi*.

The type specimen of *M. sellardsi*, UF/FGS 3822, lacks stratigraphic provenance but might be presumed to come from the Palmetto Fauna. Fortunately, we can confirm its late Hemphillian age with diagnostic material from *in situ* collections at the following four mines: an m2 from the TRO Quarry (UF 24694), an m2 from Palmetto Mine (UF 18924), a partial molar from Whidden Creek site (UF 212221), and a dentary with m2–3 from the Hardee Complex Mine (UF 102689).

GOMPHOTHERIIDAE

The two gomphothere genera in the Palmetto Fauna represent quite different evolutionary stages within that family. The larger and more progressive taxon is *R. edense*, whereas the smaller, less progressive form is *G. simplicidens*. The holotype of *Rhynchotherium simpsoni* Olsen, 1957, is an excellent palate and mandible, both with tusks. We regard this name as a junior synonym of *R. edense* (Frick, 1921) because the observed ranges of tooth size and morphology in the Palmetto Fauna sample of *Rhynchotherium* comfortably encompass those of the Mount Eden sample, which includes the holotype of *R. edense*, and because this appears to be the oldest available name for a late Hemphillian *Rhynchotherium*. Two other junior synonyms of *R. edense* that were based on Palmetto Fauna specimens are *Serridentinus brewsterensis* Osborn 1926 and *Serridentinus bifoliatus* Osborn, 1929. Olsen (1957) failed to make any comparisons between these two species and his new species. *Rhynchotherium edense* is very well represented in the Palmetto Fauna. The following specimens stand out among the available diagnostic material: an

Figure 5 *Gomphotherium simplicidens* (Osborn, 1923), left m3 in occlusal view, UF 123840.

M2 from Whidden Creek (UF 212223), paired M3s from Palmetto Mine (UF 14826), an m3 from Gardinier Ft. Meade Mine (UF 102688), a nearly complete mandible with broken tusk and m2–3 from Swift Silver City Mine (UF 24200), an upper tusk segment with spiral enamel band from Chicora Mine (UF 14984), and a juvenile dentary with dp2–p4 from the Brewster Mine (MCZ 3690; Simpson, 1930:fig. 29).

Gomphotherium simplicidens is a much smaller species with remarkably low-crowned and simply constructed cheek teeth bearing no cementum (Fig. 5). This species was originally named by Osborn (1923) for an isolated partial molar (AMNH 1907) collected at an unknown phosphate mine near Lakeland in Polk County, Florida. Occurrence of this species, with its small and primitive cheek teeth, among the very latest records of the genus appears paradoxical and demands careful documentation of its stratigraphic occurrence. Several records sustain the presence of *G. simplicidens* within the Palmetto Fauna, including an m2 (MCZ 9279) and M3 (USNM 23333) from phosphate mines near Brewster, an m3 from Whidden Creek site (UF 123840), three partial m3s from Fort Green Mine (UF 93628, 203136, and 208367), and a set of three associated, unerupted last molars, including two uppers and a lower from Peace River Mine (UF 28972).

TAPIRIDAE

Tapirids are a relatively rare component of the Palmetto Fauna. White (1942) and Olsen (1960) described a total of three specimens, but none had stratigraphic provenance. Since these pioneering efforts, about 50 tapirid specimens from the CFPD have been added to the UF collection, primarily partial maxillae and dentaries with teeth, isolated teeth, and postcrania. Some were collected *in situ* from the upper Bone Valley Formation (e.g., UF 14445, 124191, 124192, 133911, 133949, 177810, 177740, and 177814). Most of the others derive from the Palmetto, Gardinier Ft. Meade, Payne Creek, and Fort Green mines. No tapirids have been found *in situ* in the lower Bone Valley Formation, nor at any other Barstovian or early Clarendonian site in Florida for that matter.

The Palmetto Fauna tapirid specimens fall into two size categories (Fig. 6), here considered to represent distinct species. One is slightly smaller, on average, than extant *Tapirus terrestris* Linnaeus, 1758, or the Pleistocene *Tapirus veroensis* Sellards, 1918. The other is much smaller, with a cheek tooth row length about 15 to 20% shorter than *T. terrestris*, and has extremely gracile metapodials. The size of the holotype and paratype of *Tapiravus polkensis* Olsen, 1960, compares favorably with the smaller taxon, so it takes on Olsen's species name. Olsen's (1960) use of the genus *Tapiravus* Marsh, 1877, and the uncertain stratigraphy of the type specimens have led some to assume that the age of *T. polkensis* is Barstovian (e.g., Schultz et al., 1975; Schoch, 1984). Its actual chronologic range in Florida is late early to latest Hemphillian (Hulbert, 2005). The total sample of specimens from Florida is relatively limited; nevertheless, phenetically they more nearly resemble a dwarf form of *Tapirus* than true *Tapiravus* from New Jersey and Maryland (Schoch, 1984). The referral of Olsen's (1960) species to *Tapirus* is supported by phylogenetic analysis with a referred sample of *T. polkensis* from the Hemphillian Gray Fossil Site of eastern Tennessee (Hulbert and Wallace, 2005). The larger of the two Palmetto Fauna tapirids cannot be assigned to any named species of *Tapirus* and represents an undescribed species. It is currently under study by one of us (R.C.H.).

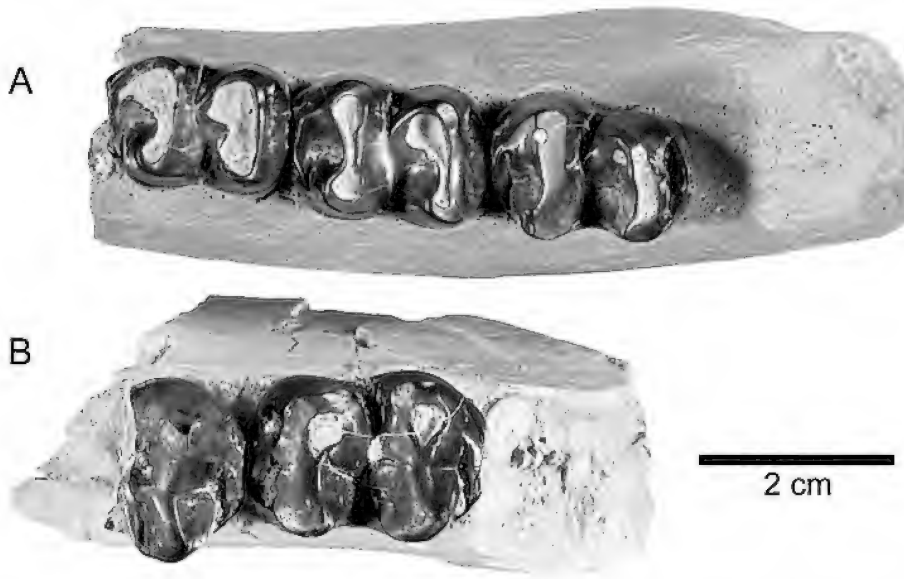

Figure 6 Tapirids: **A,** *Tapirus polkensis* (Olsen, 1960), left dentary with m1–m3 in occlusal view, UF 14445; **B,** *Tapirus* sp., left dentary with partial m1 and m2 in occlusal view, UF 18741.

RHINOCEROTIDAE

Since the mid-1960s, about 60 teeth or tooth-bearing gnathic elements and 100 postcranial bones of rhinocerotids were collected *in situ* from the upper Bone Valley Formation and are housed in the UF collections. All belong to a moderately large rhino referred to *Teleoceras hicksi* Cook, 1927, a wide-spread species known from the late early and late Hemphillian (Prothero, 1998). The Palmetto Fauna rhino has very high crowned molars and reduced premolars; p2 absent and very short lower diastema; upper molars with prominent anterior cingula, crochets, and antecrochets (Fig. 7); and lower molars lacking labial cingula. The stout limb elements are typical of the genus. Most Palmetto Fauna *Teleoceras* specimens derive from the Palmetto, Payne Creek, or Gardinier Ft.

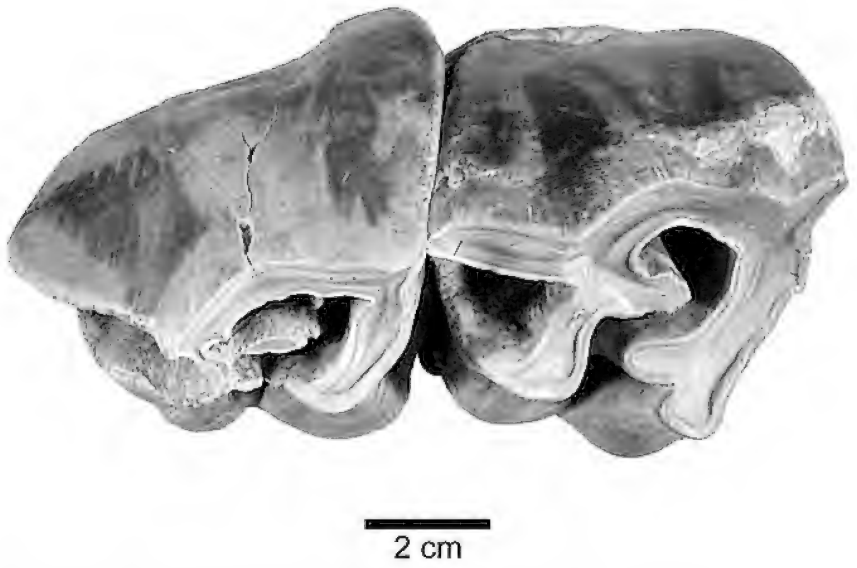

Figure 7 *Teleoceras hicksi* Cook, 1927, right M2 and M3 in occlusal view, UF 14483.

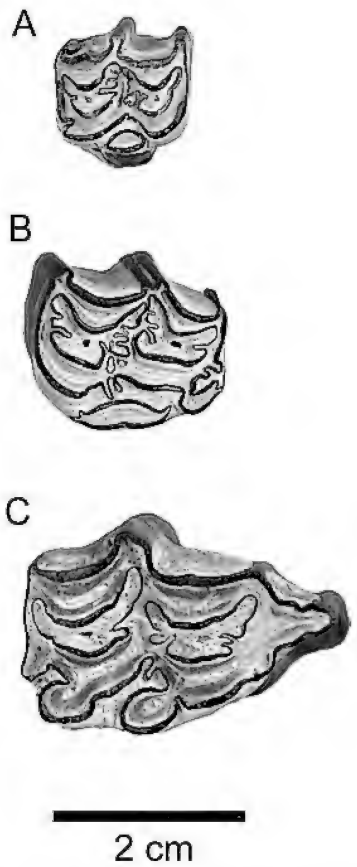

Figure 8 Equids: **A,** *Nannippus aztecus* Mooser, 1968, right M1 in occlusal view, UF 58381; **B,** *Neohipparion eurystyle* (Cope, 1893), left M3 in occlusal view, UF 207990; **C,** "*Dinohippus*" *mexicanus* (Lance, 1950), right P2 in occlusal view, UF 208602.

Meade mines, including a large sample of postcranial elements from the Whidden Creek site and several jaws from the TRO Quarry.

EQUIDAE

Remains of equids, particularly isolated teeth, are the most abundant fossils of land mammals found in the CFPD mines. The Palmetto Fauna contains six species of equids (Table 1). Over 1,200 identifiable, tooth-bearing gnathic elements and isolated teeth of Palmetto Fauna equids are in the UF and UF/FGS collections. Approximate relative abundances of the species are *Nannippus aztecus* Mooser, 1968, 44%; *Cormohipparion emsliei* Hulbert, 1988, 24%; *Pseudhipparion simpsoni* Webb and Hulbert, 1986, 15%; *Neohipparion eurystyle* (Cope, 1893), 12%; "*Dinohippus*" *mexicanus* (Lance, 1950), 5%; and *Astrohippus stockii* Lance, 1950, 0.2%. Figure 8 illustrates selected upper cheek teeth of *Nannippus aztecus*, *Neohipparion eurystyle*, and "*D.*" *mexicanus*. Numerous postcranial elements have also been collected, and those belonging to the two smallest taxa, *Nannippus aztecus* and *P. simpsoni*, can be identified to species simply on the basis of size. Overlap in size among the remaining taxa prevents their postcrania from being identified without the use of detailed morphologic and morphometric analysis. Other than *C. emsliei*, the remaining five species have wide geographic ranges and are also known from late Hemphillian faunas in Mexico and/or the southern Great Plains. The Palmetto Fauna is the only well-sampled late Hemphillian fauna that is numerically dominated by tridactyl hipparionine equids; all western faunas of this time are dominated by monodactyl equines (Webb et al., 1995).

Systematic accounts of the Palmetto Fauna equids can be found in MacFadden (1984, 1986), Webb and Hulbert (1986), and Hulbert (1987, 1988b). Their paleoecology was studied by MacFadden et al. (1999). Of their reported results, we suggest a different interpretation for *A. stockii*, which MacFadden et al. (1999) regarded as a C_3 browser. They obtained microwear and enamel carbon isotope values from only three specimens for *A. stockii*. Of these, UF 64115 is a very worn M3 with an ambiguous identification and from a different fauna (Lockwood Meadows) of a different age (early Hemphillian; Morgan, 1994). UF 64159 is a slightly worn M3 from the CFPD that lacks stratigraphic or provenance data. Its morphology is more similar to those of middle Miocene *Calippus* Matthew and Stirton, 1930, from the Bradley and Agricola faunas of the CFPD (Hulbert, 1988a). The $\delta^{13}C$ value for UF 18319, the only analyzed specimen securely identified as *A. stockii*, is significantly more positive than those of the other two specimens (MacFadden, personal communication to R.C.H.) and implies a diet predominantly of C_4 grasses, not C_3 browse.

TAYASSUIDAE

Although artiodactyls are not quite as abundant as perissodactyls in the Palmetto Fauna, they are more diverse consisting of six families and 10 genera (Table 1). The two peccaries from the Palmetto Fauna are *Catagonus brachydontus* (Dalquest and Mooser, 1980) and *Mylohyus elmorei* (White, 1942) (Wright and Webb, 1984; Wright, 1989, 1998). Nearly 70 gnathic elements with teeth or isolated teeth represent these tayassuids in the Palmetto Fauna. *Catagonus brachydontus* is more abundant, with 79% of the sample, leaving 21% to represent *M. elmorei*.

PROTOCERATIDAE

Of the five families of selenodont artiodactyls in the Palmetto Fauna, protoceratids are nearly as

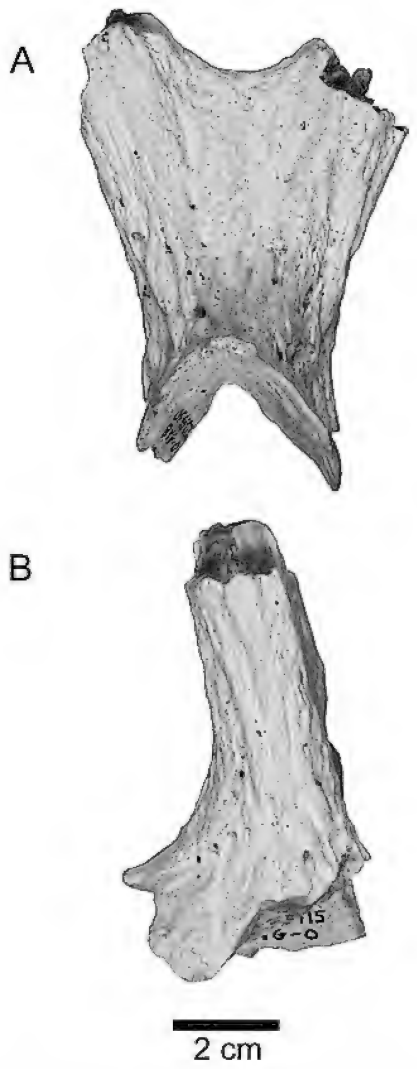

Figure 9 *Kyptoceras amatorum* Webb, 1981, nasal horn, UF 95715: **A,** anterior view; **B,** left lateral view.

rare as the much smaller gelocids. When *Kyptoceras amatorum* Webb, 1981, was first described from the CFPD, there was doubt as to whether the single known specimen was truly associated with the Palmetto Fauna (Webb, 1981). During the subsequent two decades, additional collections have confirmed that initial assignment. The supplementary sample includes 12 additional horn fragments and 12 more cheek teeth. The most remarkable of the horns is UF 95715 (Fig. 9), a low-forked nasal horn with its buttresses bridging the anterior narial opening. The dimensions of this horn are virtually identical to those of the type specimen (Webb, 1981). The additional sample of cheek teeth shows, in a manner not demonstrable in the holotype, that *K. amatorum* was considerably more hypsodont than other protoceratids. For example, crown height of each of two slightly worn m3s, UF 12248 and 55851, is 47.2 mm. A partial dentary with three molars (UF 100283) demonstrates rapid increases in size and crown height from the first to the third molar.

CAMELIDAE

Three camelid taxa are represented in the Palmetto Fauna. Each fills a distinct size range, so that the abundant camelid postcranial material can be readily sorted on the basis of size alone. The three camelids are represented by 56 isolated teeth and other dentigerous elements. In this sample, their relative abundances are *Pleiolama vera* (Matthew, 1909), 50%; *Hemiauchenia edensis* (Frick, 1921), 30%; and *Megatylopus gigas* Matthew and Cook, 1909, 20%.

The medium-sized and smaller camelids are both members of the lamine tribe. The medium-sized species is well represented by isolated teeth, dentitions, and postcranial elements, and it is readily referable to *P. vera*. This species is also present in Great Plains Hemphillian faunas such as Edson, Axtel, and Coffee Ranch (Harrison, 1979; Dalquest, 1983). Webb and Meachen (2004) recently named this genus, with *Pleiolama mckennai* from the Clarendonian of the Great Plains as its type species. *Pleiolama vera* (formerly *Hemiauchenia vera*) is the only other species in the new genus (Webb and Meachen, 2004). Recent additions of *P. vera* to the Palmetto Fauna collection, including a tibia (UF 177204) and a metacarpal (UF 212533), demonstrate the elongate limb proportions characteristic of *Pleiolama*; the length of the metacarpal is 422 mm.

The smaller llama is less familiar in the literature and is here assigned a new combination of names, *Hemiauchenia edensis*. The holotype and several referred lower jaws from Mount Eden in Southern California were assigned with a query to the genus *Procamelus* Leidy, 1858, by Frick (1921). In the Palmetto Fauna, UF 45886 and 100285 are good examples with similar mandibular morphology. The lower molars are transversely compressed and have angular lingual crescents, strong "llama buttresses," and substantial midlingual stylids. The enamel is only mildly crenulated and lacks cementum. The crown height of an unworn m3 is 24.5 mm, similar to the larger *P. vera*. The p4 is narrow with a very pronounced "lingual hook" (parastylid). The p3 is reduced with its two roots nearly fused together. The jaw shallows rapidly toward the symphysis to a minimum depth of 15 mm. A small p1 is represented by an alveolus on UF 100285. This species also occurs in the Yepómera Fauna of Mexico.

The largest and rarest camelid in the Palmetto Fauna is *M. gigas*. Previously there was some doubt as to the identity of this very large camelid,

but recent additions show convincing resemblance to the type sample of *M. gigas* from Nebraska (Matthew and Cook, 1909). The most diagnostic tooth is a P3 (UF 13216) from Swift Silver City Mine. It is three-rooted with a very weak anterolingual crest, which causes the lingual crescent to be incomplete. This feature is diagnostic of *M. gigas*, a more progressive species than *Megatylopus matthewi* Webb, 1965, from the Coffee Ranch Fauna in Texas. Also characteristic of *Megatylopus* Matthew and Cook, 1909, are two lower third incisors (UF 19254 and 133998) with extraordinarily broad and spatulate morphology. A series of right upper cheek teeth from the Whidden Creek site (UF 134000) are so heavily worn that, except for size, they lack definitive features of the species. On the other hand, a partial dentary with heavily worn molars (UF 12949) reveals the great depth of the ramus that distinguishes *Megatylopus* from equivalent-sized species of *Aepycamelus* Macdonald, 1956.

A substantial collection of podial elements also indicates affinities of this sample with *Megatylopus*. The astragali and calcanea are massive and closely resemble those of *Titanotylopus* Barbour and Schultz, 1934, that were figured and described by Breyer (1974). The proximal phalanges bear raised posterolateral ridges for strong suspensory ligaments, with the lateral ridge extending farther distally than the medial ridge. The broadly splayed distal ends of the proximal phalanges also resemble those of *Titanotylopus* as expected in a progressive species of *Megatylopus*.

GELOCIDAE

The rarest ruminant in the Palmetto Fauna is the gelocid *Pseudoceras* sp. At present, we recognize only three diagnostic specimens: a complete metatarsal, 105.5 mm in length, from the Whidden Creek site (UF 133997); the distal half of a metatarsal from Fort Green Mine (UF 43332); and a partial dentary with m1 from Palmetto Mine (UF 18530). Originally this rare genus was known only from the Great Plains and was tentatively assigned to the Camelidae (Frick, 1937). Occurrences in the Gulf Coastal Plain and assignment to the otherwise Old World Gelocidae were noted by Webb et al. (1981), Tedford et al. (1987), and, more provisionally, by Webb (1998). Tedford et al. (2004) used the first appearance of *Pseudoceras*, presumably an immigrant from Eurasia, to define the beginning of the Clarendonian. The Palmetto Fauna record extends its range beyond its previously known upper limit in the early late (Hh3) Hemphillian (Webb, 1998).

CERVIDAE

Eocoileus gentryorum Webb, 2000, is a relatively common member of the Palmetto Fauna. It is known by 56 teeth and tooth-bearing gnathic elements and thus is about as common as both antilocaprid species combined. A full account of this taxon, including a large sample of antlers, is presented by Webb (2000).

ANTILOCAPRIDAE

The Palmetto Fauna is remarkable in eastern North America for producing two endemic antilocaprid genera and species. Of 57 isolated teeth and gnathic elements, 65% represent the larger genus *Hexameryx* White, 1941, whereas 35% belong to the smaller *Subantilocapra* Webb, 1973.

Hexameryx simpsoni White, 1941, is presumably closely related to the other six-horned antilocaprid, *Hexobelomeryx fricki* Furlong, 1941, from the contemporaneous latest Hemphillian Yepómera Fauna in Chihuahua, Mexico. In their recent review of antilocaprid phylogeny, Janis and Manning (1998) agreed with Webb (1973) that subtle differences in the horncores probably warrant separation of these sibling six-horned genera. In addition to teeth and dentitions, a score of horncores representing Florida's six-horned antelope are catalogued in the UF collections. They occur in two distinct sizes and the larger form (presumed males with basal widths >30 mm) has the posterior horn set at a lower angle above the braincase (Webb, 1973). A previously undescribed juvenile specimen, UF 52424, has a posterior horncore only 11 mm in diameter at the base, but it has the proportions of an adult female horncore. That is about half of the equivalent diameter in an average adult female horncore of *H. simpsoni*. This juvenile horncore, together with the entire sample of female *H. simpsoni* horncores, shows far more consistent adherence to a standard pattern than O'Gara (1990) found in the highly variable horncores of female *Antilocapra americana* Ord, 1815. This suggests that selection for female horns was more important in the multiple-sheathed, round-horned taxa, including *Hexameryx*, that make up the Stockocerotinae of Frick (1937).

The other antilocaprid of the Palmetto Fauna is *Subantilocapra garciae* (Webb, 1973). Important new material amplifies our knowledge of this smaller, rarer pronghorn. Of particular interest are a dentary with p3–m1 from the Fort Green Mine (UF 18297; Fig. 10A) and a horncore from the Gardinier Ft. Meade Mine (UF 24004; Fig. 10B). The molar of UF 18297 indicates a well-worn stage in which the anterior fossettid has been removed. Each of the lower premolars has two deep and persistent lingual folds and a small posterior fossettid, which in an earlier wear stage would have formed a posterolingual fold. This last feature contradicts observations based on the prior, more limited sample, that a posterior fossettid did not form (Webb, 1973; Janis and Manning, 1998).

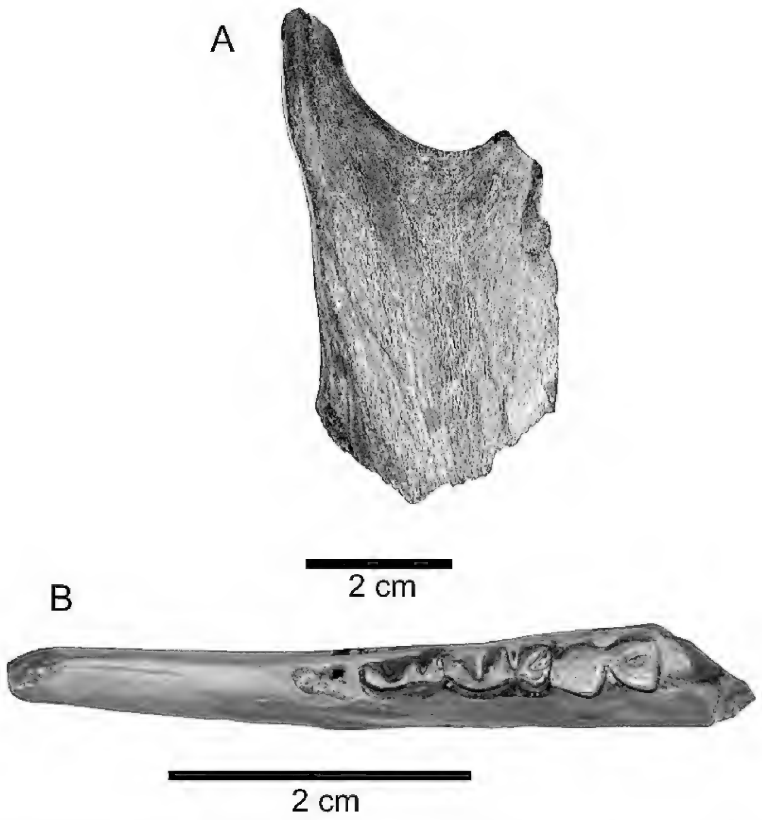

Figure 10 *Subantilocapra garciae* Webb, 1973: **A,** lateral view of right horn core, anterior to the right, UF 24004; **B,** left dentary with p3–m1 in occlusal view, UF 18297.

Development of this fossettid in later wear is a derived feature shared with *Antilocapra*.

UF 24004 is larger than previously known horncores of *S. garciae*. It measures 33.5 mm anteroposteriorly, and it is strongly compressed transversely. The horncore is broken at a point 48 mm below the notch, and the break still lies above any indication of broadening to the orbital rim. Thus, the horncore must be taller than that of *Plioceros blicki* Frick, 1937, or *Plioceros floblairi* Frick, 1937, and considerably taller than in *Texoceros* Frick, 1937. The new horncore is strongly convex laterally and concave medially, with numerous grooves and corrugations on its surface.

This strongly compressed horncore with blunt bifurcation and reduced anterior tine clearly indicates the affiliation of *Subantilocapra* with *Plioceros* on one hand and *Antilocapra* on the other. Richards and McCrossin (1991) suggested placing *Subantilocapra* within the genus *Sphenophalos* Merriam, 1909. The new evidence noted here tends to strengthen the concept that *Subantilocapra* is more progressive than either *Sphenophalos* or *Plioceros* and possibly represents the plesiomorphic sister genus of *Antilocapra*.

TAXA NOT IN THE PALMETTO FAUNA

Table 2 lists taxa regarded as belonging to the late Hemphillian Upper Bone Valley or Palmetto Fauna by previous workers, but which we do not agree, either because of misidentification or incorrect biochronology. When possible, we have re-examined the specimens in the UF/FGS, UF, MCZ, or AMNH collection upon which the original identifications were made. No specimens of any of these species have been found *in situ* from the upper Bone Valley Formation. Table 2 does not include junior synonyms of valid members of the Palmetto Fauna, such as *Neohipparion phosphorum* Simpson, 1930 (= *N. eurystyle*) or *Mammut sellardsi* (Simpson, 1930) (= *M. matthewi*).

DISCUSSION

The Bone Valley Formation, of which the upper member produces the Palmetto Fauna, consists of fluvial, estuarine, and nearshore marine sediments deposited near the southwestern edge of the Florida peninsula. Assuming that Florida remained a stable platform throughout the late

Cenozoic, the upper member of the Bone Valley Formation was deposited when sea level stood about 40 m higher than at present (Morgan, 1994), during the early Pliocene (Zanclean) sea level highstand that followed the Messinian. In his review of the effects of sea level change on Florida peninsular faunas, Emslie (1998) calculated that at times of such high sea levels, Florida occupied only 5% of its present land area.

The Palmetto Fauna, as now understood, contains 47 species of terrestrial mammals, including 18 carnivorans and 22 ungulate taxa (Table 1). How did so small a peninsula support such a diversity of large mammals? Surely climatic conditions remained seasonally mild and moist, as might be expected in a maritime peninsula with its southern tip at about 28°N. The richly productive phosphatic soils might also have helped support a bountiful ecosystem. Evidently, the coastal habitats offered an optimum balance between woodland and prairie, thus supporting a diverse mixture of browsing, mixed-feeding, and grazing ungulates (MacFadden and Cerling, 1996; MacFadden et al., 1999).

The Palmetto Fauna in part represents a Gulf Coastal refuge for elements of the Clarendonian Chronofauna (Webb et al., 1995). In the Great Plains, one finds a similar abundance of tridactyl hipparionine horses and *Teleoceras*, along with *Pseudoceras*, protoceratids, and *Gomphotherium* in Clarendonian, not Hemphillian, faunas. Compared with late Hemphillian faunas from the Great Plains, the Palmetto Fauna is notable for the persistence of diverse and abundant browsers and mix-feeders, especially mammutids, gomphotheriids, cervids, tayassuids, and tapirids. This makes the absence of the browsing rhino *Aphelops* Cope, 1873, which was common in the late Hemphillian of the Great Plains (Prothero, 1998) and was common in Florida through the late early Hemphillian, all the more puzzling. The Palmetto Fauna carnivore guild, on the other hand, is much more similar to that found in late Hemphillian faunas of the Great Plains, with only *Carpocyon* and the diverse procyonids suggesting a greater proportion of closed habitats in Florida.

The zoogeographic affinities of the Palmetto Fauna are diverse. At least two species, the squirrel *M. webbi* and the deer *E. gentryorum*, occur only in Florida, but they have their broader affinities with Eurasian taxa. These two species indicate a continuous corridor of high-latitude mesic forest from Eurasia into eastern North America during the Hemphillian (see also Wallace and Wang, 2004). The megalonychid sloth evokes a connection with South America, but *Pliometanastes* from the early Hemphillian evidently represents the original waif dispersal from which North American *Megalonyx* descended (Webb and Perrigo, 1985). No other member of the Palmetto Fauna is of South American ancestry, unlike the succeeding faunas of the Blancan Land Mammal Age. Several species within the Palmetto Fauna have probable affinities with a poorly sampled subtropical Mesoamerican fauna. This is particularly evident for *Kyptoceras*, the last of the protoceratids, for it has several Mio–Pliocene records in Mexico (Webb et al., 2003), and *Rhynchotherium*, which is first known from the late Miocene of Honduras (Webb and Perrigo, 1984). Among latest Hemphillian (= Hh4 of Tedford et al., 2004) faunas, the Palmetto Fauna most closely resembles the Mount Eden Fauna from Southern California and two faunas from Mexico, Yepómera and Rancho El Ocote. This is particularly true for many of the larger ungulates and carnivores.

Biochronologically, the Palmetto Fauna is one of the youngest Hemphillian faunas (Webb, 1981; Wright and Webb, 1984; MacFadden, 1986; Tedford et al., 1987, 2004; Morgan, 1994). Several taxa that are more typical of Blancan faunas first appear in the Palmetto Fauna, including *Mylohyus*, *Nekrolagus*, *Lynx*, and odocoileine deer represented by *Eocoileus*. The Palmetto Fauna equids *N. eurystyle*, "*D.*" *mexicanus*, *A. stockii*, and *N. aztecus* are found together elsewhere only in Hh4 faunas.

CONCLUSIONS

1. The Palmetto Fauna of central Florida includes 47 terrestrial mammalian species, including 18 carnivores and 22 ungulates. It is the richest late Hemphillian fauna in the eastern United States. We used extensive samples collected *in situ* in the upper Bone Valley Formation and the detailed mammalian biochronology of Tedford et al. (1987, 2004) to either include or exclude species from the Palmetto Fauna.
2. Ataphonomic size bias is strongly evident in favor of animals of larger body size and against those of smaller body size in the Palmetto Fauna. This is despite screenwashing large volumes of sediment at sites producing *in situ* concentrations of vertebrate fossils. While many small vertebrates were recovered by these efforts, with few exceptions they represent sharks, rays, and marine teleost fish.
3. The Palmetto Fauna differs fundamentally from similar age faunas in the western United States and Mexico. It retains a number of "holdovers" from the Clarendonian Chronofauna, including *Gomphotherium*, *Pseudoceras*, and *Carpocyon*. More than 90% of the equids are tridactyl hipparionines, as opposed to monodactyl equines. Browsers or browse-dominated mixed-feeders are relative abundant in the

Palmetto Fauna, including *Megalonyx*, *Tapirus*, *Eocoileus*, *Mylohyus*, *Catagonus*, *Mammut*, and *Gomphotherium*. Although occurring in significant numbers, they are typically outnumbered by similar-sized grazers or grass-dominated mixed-feeders (with the use of diets based on stable carbon isotopes and tooth morphology; MacFadden and Cerling, 1996; MacFadden, 1998a; MacFadden et al., 1999), including the equids, the rhino *Teleoceras*, the gomphothere *Rhynchotherium*, and the antilocaprids.

4. The carnivore component of the Palmetto Fauna generally shows less endemism and greater similarity with faunas from Mexico and the western United States than do the ungulates. Numerically, the most common carnivores are the borophagine canids, especially *Borophagus*, followed by the ursids, felids, and procyonids.
5. The following taxonomic changes are proposed for Palmetto Fauna mammals. *Mammut sellardsi* is a junior synonym of *Mammut matthewi*; *Rhynchotherium simpsoni*, "*Serridentinus*" *brewsterensis*, and "*Serridentinus*" *bifoliatus* are junior synonyms of *Rhynchotherium edense*; and "*Procamelus*" *edensis* Frick, 1921, is transferred to the genus *Hemiauchenia*. New, more complete material demonstrates that the small machairodontine felid from the Palmetto Fauna referred to *M. hesperus* by Berta and Galiano (1983) does not represent that genus or species.

ACKNOWLEDGMENTS

We are pleased to offer this synopsis of a rich terrestrial mammal fauna from Florida in honor of Dr. David P. Whistler. We have gathered inspiration from his long-term endeavors in Southern California and we see many parallels between his work and ours. During the Mio–Pliocene, mammalian faunas in North America experienced profound changes, including extinctions, immigrations, and increasing endemism. Under such circumstances, the importance of carefully documented field studies of land mammal faunas in diverse geographic provinces becomes most evident. We also note that carefully curated collections supported by libraries of maps and field notes, are crucial adjuncts to present and future programs in paleontology. We greatly appreciate Dave Whistler's strong curatorial contributions and generous treatment of visiting collaborators throughout his professional career.

This is contribution 553 in Paleobiology from the Florida Museum of Natural History (FLMNH). We thank the many students and amateurs who over the years have worked with FLMNH personnel to build a collection representing the Bone Valley faunal succession. In particular, we acknowledge John Waldrop, Norm Tessman, Don Crissinger, and Jim Ranson for their many years of bona fide service in the phosphate mines. Richard C. Hulbert, Jr., thanks C. Schaff for his assistance in the MCZ collection.

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Distribution of Pleistocene *Nothrotheriops* (Xenarthra, Nothrotheridae) in North America

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ABSTRACT. Fossil remains of the extinct ground sloth *Nothrotheriops* have been identified from 69 localities distributed throughout the western and southern United States and Mexico. These occurrences range in age from early Irvingtonian (about 1.7 Ma) to latest Rancholabrean (about 11 Ka). Most of the sites are late Pleistocene in age, and many occur in cave deposits. The paleogeographic distribution of *Nothrotheriops* is related to altitude and latitude. A bivariate plot of the elevation/latitude of localities for *Nothrotheriops* yields a distribution with a defined limit relative to elevation. A similar relationship is found when equatorial equivalent elevation (ee) is plotted against latitude. The maximum elevation for localities decreases with increased latitude and the relationship is proportional to the ee. This site elevation analysis confirms that given an apparently low basal metabolic rate for *Nothrotheriops shastensis*, climate, and specifically the minimum winter temperature, was a significant limiting factor in its geographic distribution. The association of *N. shastensis* and another thermally sensitive species, the extinct vampire bat *Desmodus stocki*, in a number of U.S. and Mexican paleofaunas suggests a similar restriction of both species by minimum winter temperatures.

INTRODUCTION

The extinct ground sloth genus, *Nothrotheriops* Hoffstetter, 1954, first appears in the North American fossil record at about 1.7 Ma in the Leisey Shell Pit 1A assemblage of Florida (McDonald, 1995). The genus is represented by two nominal species, *Nothrotheriops texanus* (Hay, 1916), which is restricted to the Irvingtonian, and *Nothrotheriops shastensis* (Sinclair, 1905), present in the Rancholabrean. *Nothrotheriops texanus* was more widespread than *N. shastensis* (see Akersten and McDonald, 1991), and it occurs in localities as far north as Oklahoma and from California to Florida (Fig. 1; Appendices 1 and 2). *Nothrotheriops shastensis* is restricted primarily to the western United States and Mexico, including the Mojave and Sonoran deserts, the southernmost Great Basin, and the northeastern edge of the Chihuahua Desert, extending south into central and western Mexico.

Nothrotheriops is the smallest of the Pleistocene North American ground sloths, which also include *Megalonyx* (Harlan, 1825), *Paramylodon* (Brown, 1903), and *Eremotherium* (Spillman, 1948). Estimates of adult mean body mass for the genus are 332 kg for the Irvingtonian species and 463 kg for the Rancholabrean species (McDonald, 2005), a difference of about 30%. *Nothrotheriops texanus* differs from *N. shastensis* (including *Nothrotheriops mexicanum* Freudenberg, 1921) in cranial and dental proportions, primarily in the relationship of alveolar length to predental length of the maxilla in the skull and alveolar length to spout length in the mandible (McDonald, 1995). Postcranially the skeletons of *N. texanus* and *N. shastensis* are similar except in size.

Nothrotheriops has been interpreted as a browser. Although no direct evidence for the diet of *N. texanus* is available, dung from *N. shastensis* is preserved in numerous dry caves in the southwestern United States. Analyses of this material have provided much detailed information on the diet of the species (Laudermilk and Munz, 1934, 1938; Martin et al., 1961; Hansen, 1978, 1980; Thompson et al., 1980; Poinar et al., 1998; Hofreiter et al., 1999). The diet of *N. shastensis* was diverse and included xeric vegetation such as globemallow (*Sphaeralcea ambigua* Gray, 1886), mormon tea (*Ephedra nevadensis* Watson, 1879), saltbrush (*Atriplex* sp. Linnaeus, 1753), and yucca (*Yucca* sp. Linnaeus, 1753) and plants associated with more mesic and riparian habitats, such as common reed (*Phragmites communis* Trinius, 1820) and singleleaf ash (*Fraxinus anomala* Watson, 1871) (Hansen, 1978). *Nothrotheriops* was probably better adapted to desert environments than any of the other North American ground sloths.

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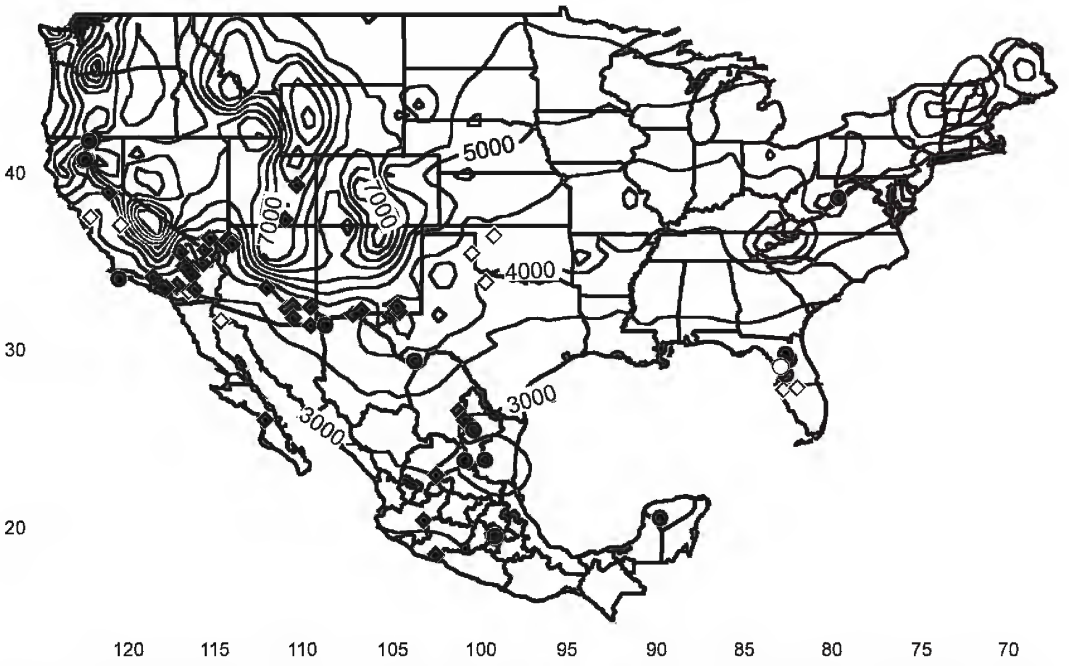

Figure 1 Paleogeographic distribution of *Nothrotheriops* Hoffstetter, 1954, and *Desmodus* Wied-Neuwied, 1824, in relation to equatorial equivalent elevation (ee) contours. ◆ = Rancholabrean *Nothrotheriops shastensis* (Sinclair, 1905); ◇ = Irvingtonian *Nothrotheriops texanus* (Hay, 1916); ● = Rancholabrean *Desmodus*; ○ = Irvingtonian *Desmodus*.

The core body temperature of *N. shastensis* was calculated as 34.4°C by Ho (1967) on the basis of amino acid ratios in its bone collagen. On the basis of its apparently low basal metabolic rate, McNab (1973) calculated that the lowest tolerable temperature limit for *N. shastensis* was 20.5°C. Akersten and McDonald (1991) and McDonald et al. (1996) pointed out that climate and, specifically, minimum temperatures might have been a significant limiting factor in the geographic distribution of *Nothrotheriops*. The present study of the relationship of site elevation and latitude (Figs. 2 and 3; Appendix 1) of localities where *Nothrotheriops* has been found confirms their assertion.

Akersten and McDonald (1991) proposed that the range reduction of *Nothrotheriops* during the Pleistocene could have resulted in a number of small disjunct populations that survived in areas of moderate to high relief. Although food resources might have been a primary controlling factor in its distribution, evidence from its distribution indicates that temperature was an equally important factor that has not been previously considered for this thermally sensitive species. Martin et al. (1961) documented that there was no apparent change in the diet of *Nothrotheriops* before its extinction and concluded that its disappearance was the result of human activity. In contrast, we conclude that the change in climate at the end of the Pleistocene from more equable conditions to those with increasing seasonal extremes was severe enough to contribute to the extinction of this thermally sensitive species.

METHODS AND MATERIALS

As part of a study on the late Pleistocene vertebrate paleoecology in the western United States, Harris (1985) calculated the equatorial equivalent (ee) of numerous faunas. The calculation of ee is based on the observation that temperature tends to decrease with both increasing latitude and elevation. An equivalent amount of temperature decrease (lapse rate) is obtained by going north 1° of latitude or increasing elevation by 107 m. With this relationship, a locality at any latitude can be converted into a hypothetical elevation above sea level at the equator, where ee = latitude (°) × 107 + elevation (m). This value permits sites to be placed in approximate relative positions to each other in terms of temperature and provides a basis for comparison. Calculation of ee does not provide any estimate of actual temperature in that many other factors come into play, such as local climatic conditions, topography, and proximity to large bodies of water (lake effect). Likewise, sea level fluctuations during the Pleistocene would have affected true temperature because lowering of sea

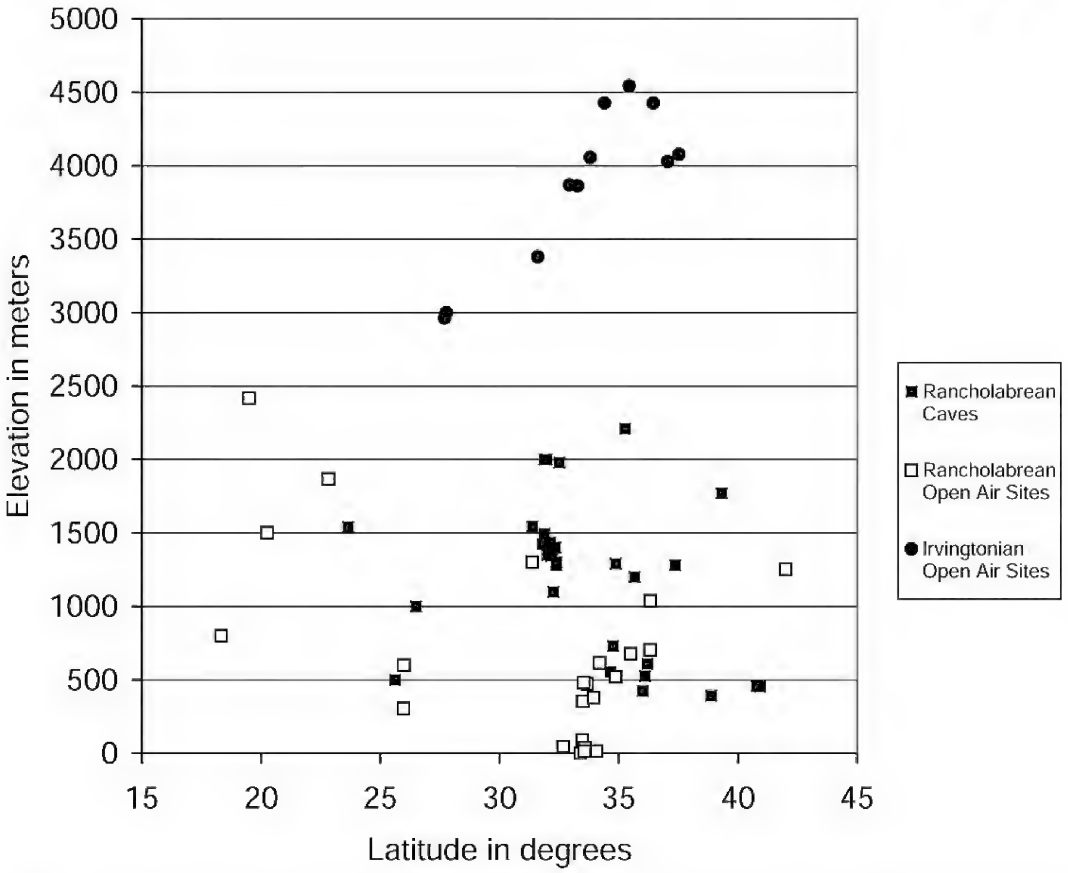

Figure 2 Bivariate distribution of elevation and latitude of localities of *Nothrotheriops* Hoffstetter, 1954. Localities from Table 1.

level effectively places all localities at higher and presumably cooler elevations. Although actual temperatures cannot be calculated, plotting the pattern of ee on a map of North America (Fig. 1) produces a general pattern of thermal gradients resulting from changes in latitude and elevation. The distribution of an individual species can then be compared against these ee isotherms to determine whether temperature appears to be one of the controlling factors in its distribution.

The ee contours shown in Figure 1 were calculated with the use of Surfer 8 by Golden Software on the basis of 599 data points. Calculation of the contour lines from the data points was done with Point Kriging. The resulting ee contours were then plotted on the base map generated by the program Mapviewer, which is produced by Golden Software.

A listing of all verified *Nothrotheriops* localities and associated information used in this analysis is presented in Appendix 1. In the process of evaluating these records, a number of spurious and/or erroneous records were found in the literature and in collections data; these are listed in Appendix 2. As part of our analysis, we have also included the distribution of another thermally sensitive species, the vampire bat *Desmodus* Wied-Neuwied, 1824 (McNab, 1973). The extinct species *Desmodus stocki* Jones, 1958, is associated with *Nothrotheriops* in a number of faunas, and it provides an independent check on our hypothesis that temperature was an important factor in the distribution and ecology of *Nothrotheriops*.

The subdivision of the Pleistocene into smaller units, such as Irvingtonian 1, Rancholabrean 2, etc. follows Repenning (1987) with the exception that late Rancholabrean 2 refers to sites within the range of radiocarbon dating (i.e., $\leq$50,000 years) and is considered equivalent to the late Pleistocene.

OBSERVATIONS AND ANALYSES

Nothrotheriops remains have been identified from at least 69 paleofaunas distributed throughout the western and southern United States and

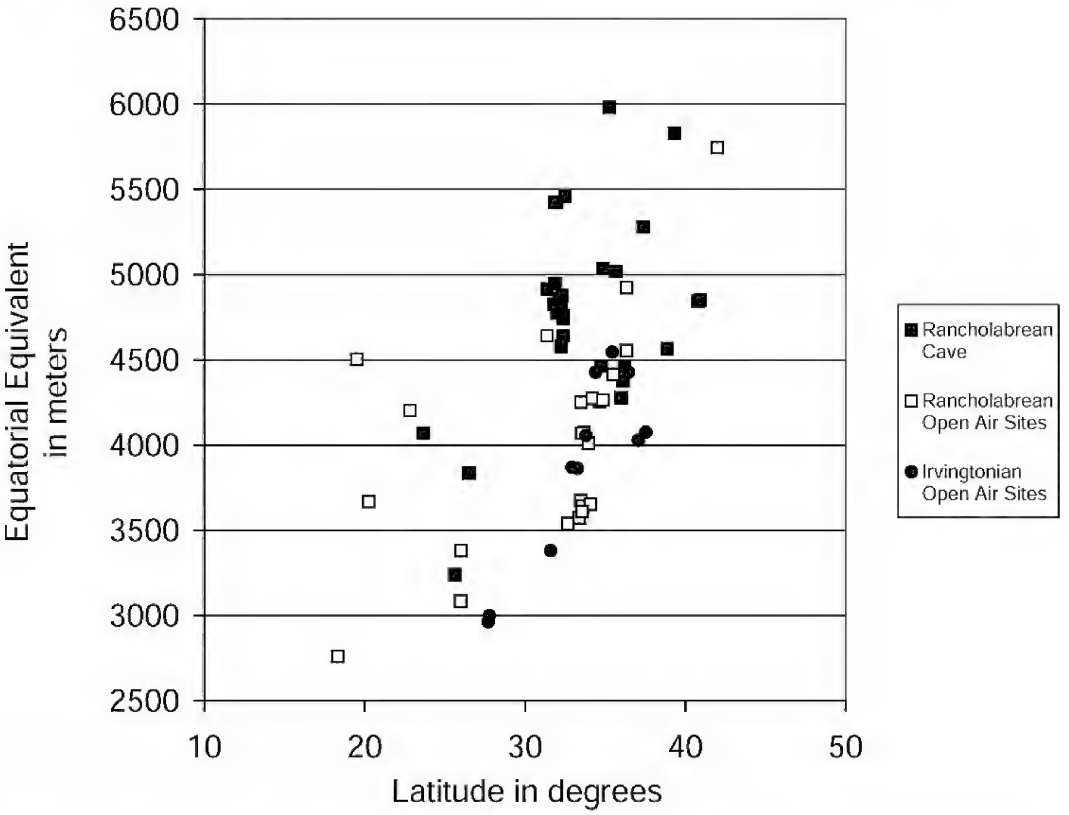

Figure 3 Bivariate distribution of equatorial equivalent elevation and latitude of localities of *Nothrotheriops* Hoffstetter, 1954. Localities from Table 1.

Table 1 Elevation and location of sites yielding *Nothrotheriops* remains. **ABBREVIATIONS: E** = elevation above mean sea level; **ee** = equatorial equivalent elevation (= elevation of the site + [107 × latitude of the site]; see Harris 1985, 1990); **La** = latitude (whole numbers are from Harris 1985); **Lo** = longitude.

Location	E (m)	ee (m)	La (°N)	Lo (°W)
Irvingtonian				
California				
1. Borrego Badlands, San Diego	305	3,864	33.27	116.33
2. Fairmead Landfill, Madera	64	4,029	37.06	120.2
3. Gypsum Ridge, San Bernardino	777	4,457	34.39	116.19
4. Irvington, Alameda	61	4,077	37.53	121.95
5. Vallecito Creek, San Diego	350	3,870	32.93	116.2
Florida				
6. Leisey 1A, Hillsborough	0	2,964	27.7	82.5
7. Pool Branch, Polk	27	3,000	27.78	81.77
Mexico				
8. El Golfo, Sonora	0	3,381	31.6	114.5
Oklahoma				
9. Curtis, Woodward	528	4,428	36.45	99
Texas				
10. Gilliland, Baylor, and Knox	440	4,057	33.8	99.46
11. Wheeler, Wheeler	753	4,545	35.44	100.25

Table 1 Continued.

Location	E (m)	ee (m)	La (°N)	Lo (°W)
Rancholabrean				
Arizona				
12. Deadman Cave, Pima	1,400	4,878	32.33	110.75
13. Kartchner Cavern, Cochise	1,423	4,826	32	110.25
14. Muav Caves, Mohave	425	4,277	36	113.87
15. Nichols Site, Maricopa	353	4,252	33.5	111.92
16. Pyeatt Cave, Cochise	1,980	5,458	32.5	110.42
17. Rampart Cave, Mohave	525	4,377	36.1	113.93
18. Ventana Cave, Pima	750	4,228	32.33	112.23
19. Whitewater Draw, Cochise	1,300	4,641	31.37	109.4
Arkansas				
20. Lower Mississippi River Valley	46	3,684	34	91
California				
21. Campbell Hill, San Bernardino	615	4,274	34.2	116.14
22. Chino Hills, San Bernardino	378	4,401	33.9	117.72
23. Diamond Valley, Riverside	471	4,075	33.68	116.99
24. Forster Ranch, Orange	91.5	3,674	33.48	117.61
25. Fort Irwin, San Bernardino	677?	4,416?	35.5	116.8?
26. Hawver Cave, El Dorado	393	4,566	38.87	120.87
27. Lake Manix, San Bernardino	520	4,265	34.87	116.5
28. Ludlow Cave, San Bernardino	554	4,256	34.56	116.1
29. Mitchell Caverns, San Bernardino	1,290	5,035	34.87	115.5
30. Newberry Cave, San Bernardino	730	4,464	34.75	116.62
31. Newport Bay Mesa, Orange	35?	3,641?	33.58	117.87
32. Pauba Mesa, Riverside	482	4,070	33.53	117.02
33. Potter Creek Cave, Shasta	457	4,844	40.78	122.28
34. Rancho La Brea, Los Angeles	15	3,653	34.07	118.35
35. Route 54 West Dire Wolf Quarry, San Diego	44	3,540	32.67	117.05
36. Salton City, Imperial	0	3,574	33.4	116?
37. Samwell Cave, Shasta	455	4,842	40.92	122.23
38. San Pedro Hill 48, Los Angeles	15?	3,610?	33.57	118.25
Mexico				
39. Bustamente Cave, Nuevo León	1,001	3,837	26.5	101
40. Cedazo, Aguascalientes	1,867	4,203	22.83	102.25
41. Cerro de la Silla Cave, Nuevo León	500	3,241	25.62	100.23
42. Comondu, Baja California Sur	305	3,085	25.98	111.97
43. Lago de Chapala, Jalisco	1,502	3,669	20.25	103
44. La Presita Cave, San Luís Potosí	1,540	4,071	23.65	100.65
45. Mina, Nuevo León	600	3,382	26	100.68
46. Rancho de La Ollas, Michoacán	800	2,161	18.33	102.27
47. San Josecito Cave, Nuevo León	2,250	4,818	23.7	99.5
48. Valley of Mexico, unknown	2,418	4,505	19.5	99.1
Nevada				
49. Devil Peak Cave, Clark	1,200	5,020	35.66	115.37
50. Gypsum Cave, Clark	610	4,462	36.2	114.2
51. Las Vegas Wash, Clark	1,037	4,924	36.33	115.17
52. Tule Springs, Clark	703	4,555	36.32	115.18
New Mexico				
53. Aden Crater, Dona Ana	1,350	4,744	32	107
54. Algerita Blossom Cave, Eddy	1,280	4,744	32.37	104.48
55. Carlsbad Caverns, Eddy	1,344	4,786	32.17	104.38
56. Conkling Cavern, Dona Ana	1,399	4,823	32.25	106.5
57. Dark Canyon Cave, Eddy	1,100	4,578	32.25	104.5
58. Dry Cave, Eddy	1,280	4,758	32.37	104.48
59. Lechuguilla Cave, Eddy	1,388	4,832	32.18	104.67
60. Sandia Cave, Sandoval	2,210	5,983	35.26	106.4
61. Shelter Cave, Dona Ana	1,453	4,859	32.12	106.5

Table 1 Continued.

Location	E (m)	ee (m)	La (°N)	Lo (°W)
62. U-Bar Cave, Hidalgo	1,545	4,916	31.37	108.62
Oregon				
63. Merrill, Klamath	1,251?	5,745?	42	121.56
Texas				
64. Dust Cave, Culberson	2,000	5,424	31.97	104.75
65. Lower Sloth Cave, Culberson	2,000	5,424	31.87	104.87
66. Upper Sloth Cave, Culberson	2,000	5,424	31.87	104.75
67. Williams Cave, Culberson	1,495	4,949	31.87	104.75
Utah				
68. Bechan Cave, Kane	1,280	5,279	37.37	110.87
69. Cowboy Cave, Wayne	1,770	5,830	39.32	110.2

Mexico (Fig. 1, Table 1). Where ages are known, most sites fall within the late Pleistocene (Irvingtonian n = 11; Rancholabrean n = 58). Many occurrences are in cave deposits (n = 43), and all cave occurrences are Rancholabrean. Localities with *Nothrotheriops* range from 42°N latitude in Oregon (Merrill, Klamath County) to as far south as 18.5°N latitude in southern Mexico (Rancho de La Ollas, State of Michoacán). The elevation of localities ranges from to 2,250 m above mean sea level (San Josecito Cave, State of Nuevo León, Mexico) to near sea level in California and Florida (Table 1).

Examination of the relationship of elevation and latitude of localities with *Nothrotheriops* indicates that the maximum elevation at which the genus is found decreases with increasing latitude (Fig. 2). A similar relationship is found when ee (m) is plotted against latitude (Fig. 3). Although the number of pre-Rancholabrean 2 sites is very limited (n = 11), the distribution of all age sites through time, relative to elevation,

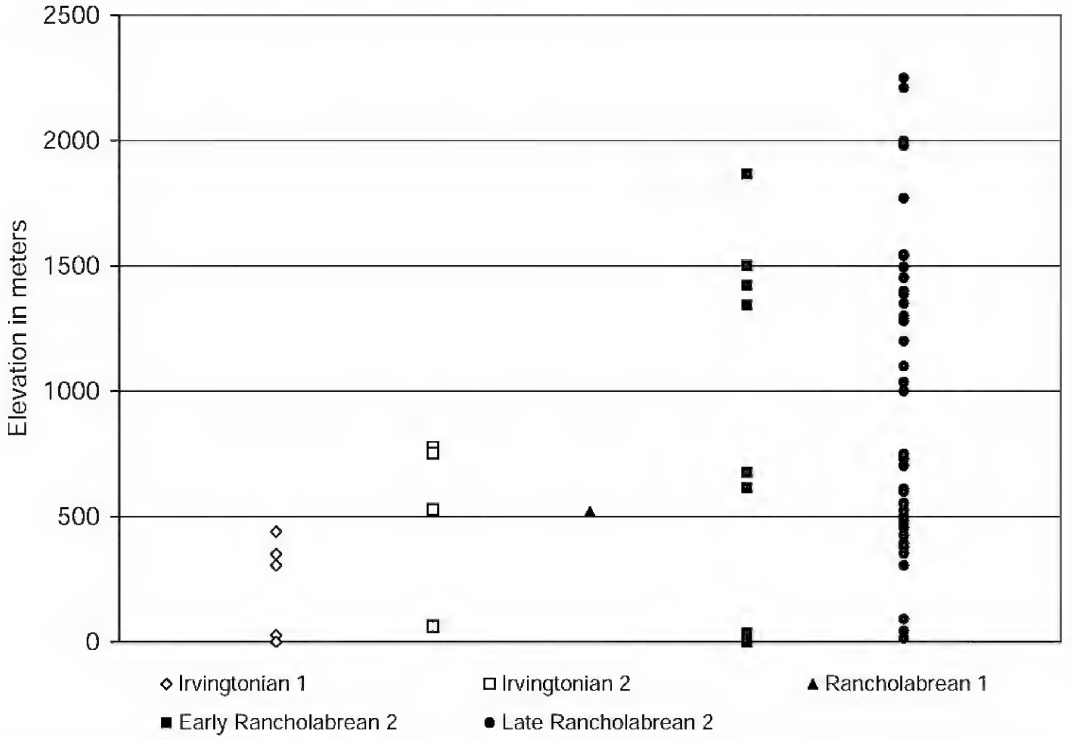

Figure 4 Bivariate distribution of the age and elevation of localities of *Nothrotheriops* Hoffstetter, 1954. Localities and data from Table 1.

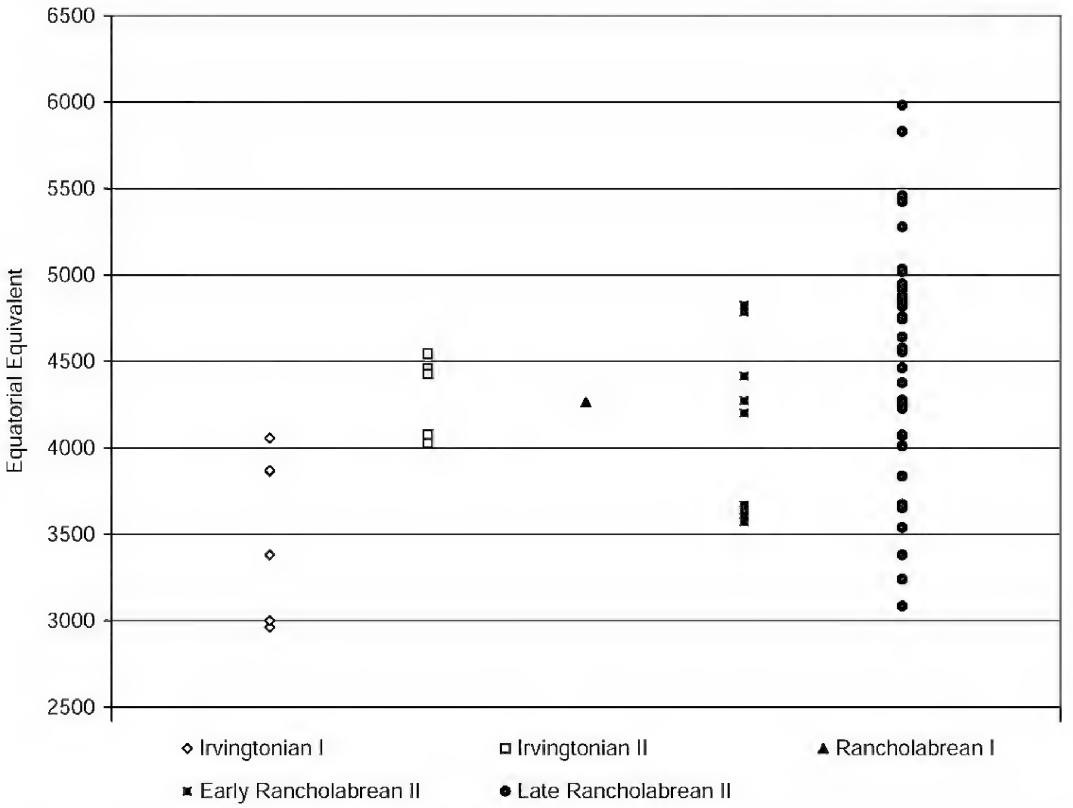

Figure 5 Bivariate distribution of the age and equatorial equivalent elevation of localities of *Nothrotheriops* Hoffstetter, 1954. Localities from Table 1.

exhibits an increased frequency of both higher elevation localities with decreasing age (Fig. 4) and an increased ee with decreasing age (Fig. 5). This apparent trend suggests that *Nothrotheriops* might have become more tolerant to cooler conditions, adapting (physiologically or behaviorally) to higher elevation environments during the Pleistocene. The distribution of ee values for localities with *Nothrotheriops* approximates a bell-shaped curve for both the Rancholabrean and Irvingtonian (Fig. 6), but the mean for the Rancholabrean sites has shifted. During the Irvingtonian, the mean is between 4,001 and 4,500 m ee, whereas in the Rancholabrean it is between 4,501 and 5,000 m ee. As noted before, the body size of *Nothrotheriops* in the Rancholabrean is greater than in the Irvingtonian and might have conferred more thermal inertia, permitting this shift into cooler habitats.

Two important outliers in the data are the Rancholabrean records of *Nothrotheriops* from Merrill, Oregon, and Cowboy Cave, Utah. Both of these localities have the highest ee values for the genus and represent the extremes with regard to latitude: 42°N and 39.32°N, respectively. The Oregon record is based on a single phalanx, which is not particularly diagnostic. The Cowboy Cave record is based on dung and hair. The only other Utah record, from Bechan Cave, based on dung and hair, falls into the same ee category as cave sites in the Guadalupe Mountains of Texas, where the presence of *Nothrotheriops* is also based on dung records.

Noncave sites that yield *Nothrotheriops* remains range in ee from about 2,900 to 4,900 m, and the ee of cave sites with *Nothrotheriops* range from about 3,800 to 5,800 m, with an overlap in the distribution between 3,800 and 4,900 m. The observation that most low ee sites are open and most high ee sites are caves implies that *Nothrotheriops* more frequently occupied caves at cooler, higher altitudes during later Pleistocene time. If caves were necessary to serve as thermal buffers and den sites, then they would have been a limiting factor to the animal's distribution despite an otherwise abundant food supply. The result would be a patchy Rancholabrean distribution because the distribution of caves is random.

The extinct vampire bat *D. stocki* is associated with *N. shastensis* at five late Pleistocene cave sites: La Presita Cave, Potter Creek Cave,

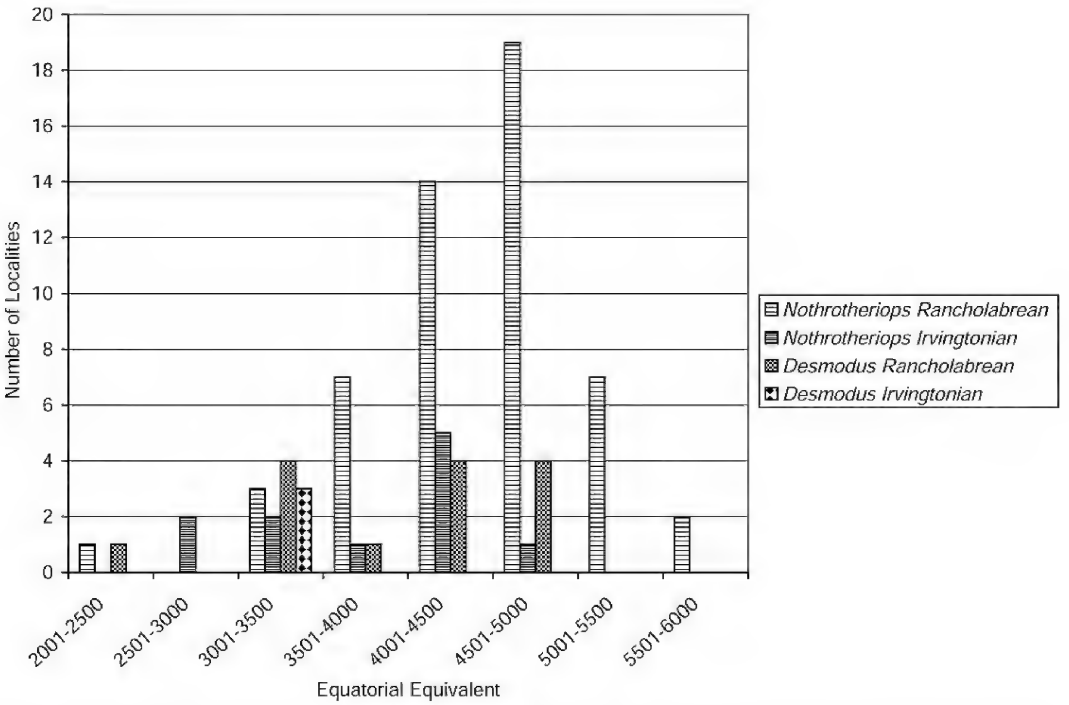

Figure 6 Relative frequency distribution of the equatorial equivalent for faunas with *Nothrotheriops* Hoffstetter, 1954, and *Desmodus* Wied-Neuwied, 1824. Localities from Tables 1 and 2.

Table 2 Elevation and location of sites yielding the remains of *Desmodus*. **ABBREVIATIONS: E** = elevation above mean sea level; **ee** = equatorial equivalent elevation (= elevation of the site + [107 × latitude of the site]; see Harris 1985, 1990); **La** = latitude (whole numbers are from Harris 1985); **Lo** = longitude.

Location	E (m)	ee (m)	La (°N)	Lo (°W)
Irvingtonian				
Haile 16A, FL	24	3,202	29.7	82.4
Haile 21A, FL	24	3,202	29.7	82.4
Inglis 1A, FL	0	3,103	29	82.7
Rancholabrean				
Arredondo, FL	21	3,081	28.6	82.4
Cerro de Tlapacoya, MX	2,240	4,305	19.3	98.92
Cueva de la Boca, MX	540	3,260	25.42	100.15
Cueva La Presita, MX	1,540	4,071	23.65	100.65
Haile, FL	24	3,202	29.7	82.4
Little Thirty Eight Mine, TX	~946	4,084	29.33	103.66
Lotun, MX	40	2,223	20.4	89.53
New Trout Cave, WV	570	4,700	38.6	79.4
Potter Creek Cave, CA	457	4,844	40.78	122.8
Rampart Cave, AZ	525	4,377	36.1	113.93
Reddick, FL	24	3,170	29.4	82.2
San Josecito Cave, MX	2,250	4,818	23.7	99.5
San Miguel Island, CA	~10	3,652	34.04	120.33
U-Bar Cave, NM	1,545	4,916	31.37	108.62

Rampart Cave, San Josecito Cave, and U-Bar Cave. Additional fossil vampire bat records include *D. stocki* (at Reddick 1A, Florida; Cueva de La Boca, State of Nuevo Leon; and Tlapacoya, State of Mexico) and *Desmodus* cf. *Desmodus draculae* Morgan, Linares, and Ray, 1988; *Desmodus rotundus* Wied-Neuwied, 1824; and *Diphylla ecaudata* Spix, 1823 (at Gruta de Lotun, State of Yucatan, Mexico) (Arroyo-Cabrales and Ray, 1997; Grady et al., 2002) (Table 2). Modern *D. rotundus* ranges through coastal northern and all southern Mexico, but the northern extent of its ranges is restricted to the 10°C minimal winter isotherm (McNab, 1973).

The association of *N. shastensis* and *D. stocki* in a number of paleofaunas and a general similarity in the paleogeographic ranges of these taxa (Fig. 1) suggest a similar restriction in the distribution of both species by winter temperatures. As shown in Figure 6, ee distributions for both the sloth and bat overlap during both the Irvingtonian and Rancholabrean. The vampire bat, however, was more restricted by cooler temperatures, and its maximum ee value is 4,916 at U-Bar Cave. Other factors besides temperature would have determined the distributional association of the Shasta ground sloth and vampire bat besides temperature. These might have included area of overlapping availability of caves as roost sites for the bat (all five associations of the sloth and bat are from cave sites) and types of vegetation used as food by the sloth.

The presence of *D. stocki* from late Pleistocene deposits (layers dated at 28,250 ± 850 and older than 29,400 ± 1,700 years BP) in New Trout Cave, West Virginia (Grady et al., 2002), a time when the range of *Nothrotheriops* was restricted to western North America, indicates that the vampire bat did not undergo a range reduction similar to that of the Shasta ground sloth during the Pleistocene. Given our knowledge of the diet and preferred habitat of *Nothrotheriops*, it is not surprising that it is not found in the eastern deciduous forests. Food was probably not a limiting factor for the vampire bat because it could have fed on blood from other members of the Pleistocene megafauna besides the Shasta ground sloth. The vampire bat from New Trout Cave is associated with amphibians, reptiles, and mammals indicative of mild winters and warm summers (Grady et al., 2002). Although New Trout Cave is at 38°39′09″N, with an elevation of 570 m, its ee is 4,700 m, values similar to that of localities with *Nothrotheriops* in the west at the same time.

CONCLUSIONS

1. Northern localities that yield *Nothrotheriops* remains always occur at elevations lower than more southern localities, and the relationship is proportional to ee. Given that higher altitudes have cooler temperatures, relative to latitude, this observation strongly suggests that minimum winter temperatures was the primary limiting factor to the northern extent of the paleogeographic range of *Nothrotheriops* and not other ecological factors. The fact that most low ee sites are not caves and most high ee sites are caves and that the number of cave sites are more numerous during later Pleistocene time is probably not merely an accident of preservation. This relationship might indicate that *Nothrotheriops* more frequently occupied caves during the later Pleistocene as a possible thermoregulatory behavior to avoid seasonally lower temperatures at higher elevations. Over the year, cave temperatures are relatively stable compared with outside temperatures and often approximate the mean annual temperature of the region (Hill and Forti, 1997); thus, caves can serve as a thermal buffer during cold periods. On the basis of its lower than expected body temperature for its size, McNab (1985) calculated that below 20.5°C *Nothrotheriops* would have had to increase its metabolism to generate heat. Moving into a cave during cold periods would have reduced the thermal gradient and the related metabolic cost. If such a behavioral strategy were adopted in the late Pleistocene, this would indicate that caves played a critical role in the animal's ecology and account for the high incidence of its preservation in caves.
2. The association of *N. shastensis* and *D. stocki* in a number of assemblages suggests a similar latitudinal and altitudinal restriction of both species by minimal winter temperatures. Given the sloth's low metabolic rate and the thermal restrictions exhibited by modern vampire bats, this lower limiting temperature falls in the range of 10 to 20°C.

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APPENDICES

Appendix 1 *Nothrotheriops* remains, dates, and/or relative ages for each documented locality. Numbers in parentheses refer to Table 1. Selected references are included. Irvingtonian I (1.9–0.9 Ma), Irvingtonian II (0.9–0.4 Ma), Rancholabrean I (0.4 Ma–150 Ka), early Rancholabrean II (150–50 Ka), late Rancholabrean II (50–10 Ka).

ARIZONA

Deadman Cave, Pima County (12)
- Identification: *Nothrotheriops shastensis*
- Age: late Rancholabrean II
- Material: dental
- Repository: University of Arizona Laboratory of Paleontology, Tucson, Arizona
- Reference: Mead et al. (1984)

Kartchner Cave, Cochise County (13)
- Identification: *Nothrotheriops shastensis*
- Age/Date: early Rancholabrean II, 85,000 BP uranium age date series
- Repository: Quaternary Studies Program, Northern Arizona University, Flagstaff, Arizona

Muav Caves, Mohave County (14)
- Identification: *Nothrotheriops shastensis*
- Age/Date: late Rancholabrean II, 11,810 ± 70 to 10,650 ± 220 BP ^{14}C
- Material: skeletal, dung, skin/hair
- Repositories: National Park Service, Grand Canyon, Arizona; University of Arizona Laboratory of Paleontology, Tucson, Arizona
- References: Long and Martin (1974), Harris (1985), Martin et al. (1985), Meltzer and Mead (1985), Mead and Agenbroad (1992)

Nichols Site, Maricopa County (15)
- Identification: ?*Nothrotheriops* sp.
- Age/Date: late Rancholabrean II
- Material: skeletal
- Repository: University of Arizona Laboratory of Paleontology, Tucson, Arizona
- References: Lindsay and Tessman (1974), Harris (1985)

Pyeatt Cave, Cochise County (16)
- Identification: *Nothrotheriops shastensis*
- Age/Date: late Rancholabrean II
- Material: skeletal
- Repository: University of Arizona Laboratory of Paleontology, Tucson, Arizona
- References: Lindsay and Tessman (1974), Harris (1985)

Rampart Cave, Mohave County (17)
- Identification: *Nothrotheriops shastensis*
- Age/Date: late Rancholabrean II, >40,000–9,900 ± 400 BP, average 11,070 BP ^{14}C
- Material: skeletal, dung, hair/skin
- Repositories: U.S. National Museum, Washington, D.C.; National Parks Service, Grand Canyon, Arizona
- References: Wilson (1942), Martin et al. (1961, 1985), Harrington (1972), Lindsay and Tessman (1974), Long and Martin (1974), Hansen (1978), Kurtén and Anderson (1980), Thompson et al. (1980), Harris (1985), Emslie (1987), Graham and Mead (1987), Mead and Agenbroad (1992)

Ventana Cave, Pima County (18)
- Identification: *Nothrotheriops shastensis*
- Age/Date: late Rancholabrean II, 11,300 ± 1,200 to 8,980 ± 300 BP ^{14}C
- Material: skeletal
- Repositories: American Museum of Natural History, New York, New York; Museum of Northern Arizona, Flagstaff, Arizona
- References: Colbert (1950, 1975), Martin (1967), Lindsay and Tessman (1974), Kurtén and Anderson (1980), Harris (1985), Meltzer and Mead (1985)

Whitewater Draw (Whitewater Wash), Cochise County (19)
- Identification: *Nothrotheriops shastensis*
- Age/Date: late Rancholabrean II, <15,000 BP ^{14}C
- Repository: University of Arizona Laboratory of Paleontology, Tucson, Arizona
- References: Waters (1986), Graham et al. (1995)

ARKANSAS

Mississippi River Valley, Arkansas County (20)
- Identification: *Nothrotheriops* sp.
- Age/Date: early Rancholabrean?
- Material: skeletal
- Repository: Pink Palace Museum, Memphis, Tennessee
- Reference: McDonald and Ruddell (personal communication, 2002)

CALIFORNIA

Borrego Badlands, San Diego County (1)
- Identification: ? *Nothrotheriops* sp.
- Age/Date: Irvingtonian II, mid Irvingtonian
- Material: skeletal
- Repository: Colorado Desert District Stout Research Center, Borrego Springs, California
- Reference: Remeika and Jefferson (1995)

Campbell Hill, San Bernardino County (21)
- Identification: *Nothrotheriops* sp.
- Age/Date: ?Rancholabrean
- Material: skeletal
- Repository: Natural History Museum Los Angeles County, Los Angeles, California
- References: Bacheller (1978), Jefferson (1991, 1992)

Chino Hills, San Bernardino County (22)
- Identification: *Nothrotheriops* sp.
- Age/Date: Rancholabrean?
- Material: skeletal

Repository: Natural History Museum Los Angeles County, Los Angeles, California
References: unpubilished

Diamond Valley, Riverside County (23)
Identification: *Nothrotheriops shastensis.*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: San Bernardino County Museum, Redlands, California
Reference: This paper

Fairmead Landfill, Madera County (2)
Identification: *Nothrotheriops* cf. *N. shastensis*
Age/Date: Irvingtonian II; early Bruhnes Magnetochron
Material: skull and tooth
Repository: University of California Museum of Paleontology, Berkeley, California
Reference: Dundas et al. (1996)

Forster Ranch, Orange County (24)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: San Bernardino County Museum, Redlands, California
Reference: Stadum (1996)

Fort Irwin, San Bernardino County (25)
Identification: *Nothrotheriops* sp.
Age/Date: ?Rancholabrean I
Material: skeletal
Repository: San Bernardino County Museum, Redlands, California
References: Reynolds and Woodburne (1987), Jefferson (1991)

Gypsum Ridge, San Bernardino County (3)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian II
Material: skeletal
Repository: San Diego Natural History Museum, San Diego, California
Reference: Wagner (2002)

Hawver Cave, El Dorado County (26)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II; late Wisconsinan
Material: skeletal
Repository: University of California Museum of Paleontology, Berkeley, California
References: Stock (1918), Hay (1927), Kurtén and Anderson (1980), Lundelius et al. (1983), Jefferson (1991)

Irvington, Alameda County (4)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian II
Material: skeletal
Repository: University of California Museum of Paleontology, Berkeley, California
References: Savage (1951), McDonald (1995)

Lake Manix, San Bernardino County (27)
Identification: *Nothrotheriops* cf. *N. shastensis*
Age/Date: Rancholabrean I, ~200 Ky BP, tephrochronology and U/Th series (below Long Canyon Ash 1.85 Ma, above 350+ Ka U/Th)
Material: skeletal
Repositories: Department of Geological Sciences, University of California, Riverside, California; Natural History Museum of Los Angeles County, Los Angeles, California; San Bernardino County Museum, Redlands, California; University of California Museum of Paleontology, Berkeley, California
References: Kurtén and Anderson (1980), Jefferson (1985, 1987, 1991, 2003)

Ludlow Cave (Two Raven Cave), San Bernardino County (28)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, Wisconsinan
Material: skeletal
Repository: San Bernardino County Museum, Redlands, California
Reference: Jefferson (1991)

Mitchell Caverns, San Bernardino County (29)
Identification: *Nothrotheriops* sp.
Age/Date: late Rancholabrean II, Wisconsinan
Material: skeletal
Repository: California State Museum Resources Center, Sacramento, California
Reference: Jefferson (1991)

Newberry Cave, San Bernardino County (30)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 11,600 ± 500 BP ^{14}C
Material: partial skeleton
Repository: San Bernardino County Museum, Redlands, California
References: Davis and Smith (1981), Jefferson (1991)

Newport Bay Mesa, Los Angeles County (31)
Identification: *Nothrotheriops shastensis*
Age/Date: early Rancholabrean II, Sangamon; 130–120,000 BP, OIS 5e
Material: skeletal
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
References: Miller (1971), Kurtén and Anderson (1980), Jefferson (1991)

Pauba Mesa, Riverside County (32)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Repository: San Bernardino County Museum, Redlands, California
Reference: Stadium (1996)

Potter Creek Cave, Shasta County (33)
Identification: *Nothrotheriops shastensis* (type)
Age/Date: late Rancholabrean II, Wisconsinan to 8,250 ± 330 BP ^{14}C
Material: skeletal, dental
Repository: University of California Museum of Paleontology, Berkeley, California
References: Sinclair (1905), Stock (1918), Hay (1927), Hutchison (1967), Kurtén and Anderson (1980), Lundelius et al. (1983)

Harris (1985), Meltzer and Mead (1985), Jefferson (1991)

Rancho La Brea, Los Angeles County (34)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, locality (pit No.) 3, >28,000–12,650 ± 160 BP; locality (pit No.) 61/67, 12,200 ± 200 to 11,130 ± 275 BP; locality (pit No.) 91, 35,735 ± 4,050 to 25,100 ± 850 BP ^{14}C
Material: skeletal, dental
Repositories: George C. Page Museum, Los Angeles, California; Natural History Museum of Los Angeles County, Los Angeles, California; University of California Museum of Paleontology, Berkeley, California
References: Stock (1992), Kurtén and Anderson (1980), Marcus and Berger (1984), Jefferson (1991)

Route 54 West "Dire Wolf" Quarry, San Diego County (35)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: San Diego Museum of Natural History, San Diego, California
Reference: This paper

Salton City, Imperial County (36)
Identification: *Nothrotheriops* sp.
Age/Date: ?Rancholabrean
Material: skeletal
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
References: McDonald (1985), Jefferson (1991)

Samwell Cave, Shasta County (37)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 17,880 ± 900 to 15,360 ± 500 BP ^{14}C
Material: skeletal
Repository: University of California Museum of Paleontology, Berkeley, California
References: Stock (1918), Hay (1927), Kurtén and Anderson (1980), Lundelius et al. (1983), Harris (1985)

San Pedro Hill 48, Los Angeles County (38)
Identification: *Nothrotheriops* cf. *N. shastensis*
Age/Date: early Rancholabrean II, Sangamon; 130–120,000 BP, Oxygen isotope stage 5e
Material: skeletal
Repository: Natural History Museum of Los Angeles County, California
References: Miller (1971), Langenwalter (1975), Kurtén and Anderson (1980), Jefferson (1991)

Vallecito Creek, San Diego County (5)
Identification: *Nothrotheriops* cf. *N. texanus*
Age/Date: Irvingtonian I
Material: skeletal
Repository: Colorado Desert District Research Center, Borrego Springs, California
References: Downs and White (1966, 1968), Opdyke et al. (1977), McDonald (1995), Remeika et al. (1995), Cassiliano (1999)

FLORIDA

Leisey 1A, Hillsborough County (6)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian I, 1.07–1.55 Ma BP, magnetochronologic, strontium isotope
Material: skeletal, dental
Repository: Florida Museum of Natural History, Gainesville, Florida
Reference: McDonald (1995)

Pool Branch, Polk County (7)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian I
Material: skeletal
Repository: Florida Museum of Natural History, Gainesville, Florida
References: McDonald (1985, 1995)

MEXICO

Bustamente Cave, Nuevo León (39)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: Texas Memorial Museum, Austin, Texas
References: McDonald (1985), M. Winans (personal communication, 1991)

Cedazo, Aguascalientes (40)
Identification: *Nothrotheriops shastensis*
Age/Date: early Rancholabrean II, Sangamonian
Material: skeletal
Repositories: Instituto de Geológica Universidad Nacional Autónoma de México D.F.; Mooser, private collection
Reference: Kurtén and Anderson (1980)

Cerro de La Silla Cave, Nuevo León (41)
Identification: *Nothrotheriops* sp.
Age/Date: late Rancholabrean II
Material: dental
Repository: Museum of Paleontology, University of California, Berkeley, California
References: Furlong (1925), Silva-Barcenas (1969)

Comondu, Baja California Sur (42)
Identification: *Nothrotheriops* sp.
Age/Date: Rancholabrean II
Material: skeletal, dental
Repository: Brigham Young University, Provo, Utah
References: W. Miller (personal communication, 1993, 1996), McDonald (1995)

El Golfo, Sonora (8)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian I
Material: skeletal
Repositories: Instituto de Geológica Universidad Nacional Autónoma de México D.F.; Natural History Museum of Los Angeles County, Los Angeles, California; San Diego Natural History Museum, San Diego, California

References: Shaw (1981), McDonald (1995)

Lago de Chapala, Jalisco (43)
Identification: *Nothrotheriops* sp.
Age/Date: Rancholabrean II
Material: skeletal
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
Reference: Downs (1958)

La Presita Cave, San Luís Potosí (44)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: dental
Repository: Laboratorio de Paleozoología de la Subdirección de Servicios Académicos del Instituto Nacional de Antropología e Historia, Mexico, D.F.
Reference: Polaco and Butrón (1997)

Mina 1, Nuevo León (45)
Identification: *Nothrotheriops shastensis*
Age/Date: Rancholabrean II
Material: skeletal, dental
Repositories: Museo Bernabé de las Casas, Mina, Mexico, D.F.; Facultad de Ciencias de la Terra, Peter Meiburg Museo Geológico Regional, Linares, Nuevo León, Mexico, D.F.
Reference: Franzen (1994)

Rancho de La Ollas, Michoacán (46)
Identification: *Nothrotheriops* sp.
Age/Date: Rancholabrean II
Material: not identified
Repository: not identified
Reference: Silva-Barcenas (1969)

San Josecito Cave, Nuevo León (47)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, Wisconsinan; 45,000–11,000 BP ^{14}C
Material: skeletal, dental
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
References: Kurtén and Anderson (1980), Harris (1985), Arroyo-Cabrales et al.(1995)

Valley of Mexico (48)
Identification: *Nothrotheriops shastensis* (type *N. mexicanum*)
Age/Date: unknown
Material: skeletal
Repository: present location of type unknown, cast of specimen in the Museum of Paleontology, University of California, Berkeley, California
Reference: Freudenberg, 1921

NEVADA

Devil Peak Cave, Clark County (49)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, late Wisconsinan
Material: skeletal, dental
Repository: San Bernardino County Museum, Redlands, California
Reference: Reynolds et al. (1991)

Gypsum Cave, Clark County (50)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 33,910 ± 3,720 to 11,360 ± 260 BP ^{14}C
Material: skeletal
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
References: Harrington (1933), Kurtén and Anderson (1980), Thompson et al. (1980); Grayson (1982), Harris (1985), Martin et al. (1985), Meltzer and Mead (1985)

Las Vegas Wash, Clark County (51)
Identification: *Nothrotheriops* sp.
Age/Date: late Rancholabrean II, >23,800 BP ^{14}C
Material: skeletal
Repository: American Museum of Natural History, New York, New York
References: Simpson (1933), Hester (1960), McDonald (1995)

Tule Springs, Clark County (52)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, Unit B-2, >40,000 BP ^{14}C
Material: skeletal
Repositories: American Museum of Natural History, New York New York; Natural History Museum of Los Angeles County, Los Angeles, California; University of California Museum of Paleontology, Berkeley, California
References: Martin (1967), Mawby (1967), Kurtén and Anderson (1980), Grayson (1982), Harris (1985)

NEW MEXICO

Aden Crater (Aden Fumarole), Dona Ana County (53)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 11,080 ± 200 and 9,840 ± 160 BP ^{14}C
Material: skeletal, dung, skin/hair
Repository: Yale Peabody Museum, New Haven, Connecticut
References: Lull (1929), Simons and Alexander (1964), Martin (1967), Long and Martin (1974), Kurtén and Anderson (1980), Harris (1985), Martin et al. (1985), Meltzer and Mead (1985)

Algerita Blossom Cave, Eddy County (54)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: University of Texas, El Paso, Texas
Reference: A. Harris (personal communication, 1996)

Carlsbad Caverns, Eddy County (55)
Identification: *Nothrotheriops shastensis*
Age/Date: early Rancholabrean II, 111,900 ± 13,300–11,700 BP, U/Th series
Material: skeletal

Repository: National Park Service, Carlsbad Caverns, New Mexico
Reference: Hill and Gillette (1985, 1987)

Conkling Cavern, Dona Ana County (56)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
References: Conkling (1932), Lundelius et al. (1983), Harris (1985)

Dark Canyon Cave, Eddy County (57)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: University of Nebraska State Museum, Lincoln, Nebraska
Reference: Harris (1985)

Dry Cave (Animal Fair, Charlies Parlor, Hampton Court), Eddy County (58)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 15,030 ± 210 BP ^{14}C
Material: skeletal
Repository: University of Texas, El Paso, Texas
References: Harris (1970, 1985), Kurtén and Anderson (1980), Lundelius et al. (1983), Meltzer and Mead (1985)

Lechuguilla Cave, Eddy County (59)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: National Park Service, Carlsbad Caverns, New Mexico
Reference: P. Jablonsky (personal communication, 1995)

Sandia Cave, Sandoval County (60)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: Maxwell Museum of Anthropology, University of New Mexico, Albuquerque, New Mexico
References: Hibben (1941), G. Morgan (personal communication, 2003)

Shelter Cave, Dona Ana County (61)
Identification: *Nothrotheriops* sp.
Age/Date: late Rancholabrean II, 12,430 ± 190 to 11,330 ± 370 BP ^{14}C
Material: skeletal, dung
Repository: Natural History Museum of Los Angeles County, Los Angeles, California
References: Thompson et al. (1980), Lundelius et al. (1983), Harris (1985), Martin et al. (1985), Meltzer and Mead (1985), Graham and Mead (1987)

U-Bar Cave, Hidalgo County (62)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II 13,030 ± 180 BP ^{14}C
Material: skeletal
Repository: University of Texas, El Paso, Texas
References: Harris (1985), Emslie (1987)

OKLAHOMA

Curtis (Quinlan), Woodward County (9)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian II
Material: skeletal
Repository: National Museum of Natural History, Washington, D.C.
References: Akersten and McDonald (1991), McDonald (1995)

OREGON

Merrill, Klamath County (63)
Identification: *Nothrotheriops sp.*
Age/Date: Pleistocene
Material: skeletal
Repository: Department of Geology, Oregon State University, Corvallis, Oregon
Reference: Packard (1952)

TEXAS

Dust Cave, Culbertson County (64)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II
Material: skeletal
Repository: University of Texas, El Paso, Texas
Reference: Harris (1985)

Gilliland, Baylor and Knox Counties (10)
Identification: *Nothrotheriops texanus*
Age/Date: Irvingtonian I; 1.2–1.5 Ma BP, tephrochronology (below Type O Ash = Lava Creek B, 0.61 Ma)
Material: skeletal
Repository: Museum of Paleontology, University of Michigan, Ann Arbor, Michigan
References: Hibbard and Dalquest (1966), McDonald (1995)

Lower Sloth Cave (Cave 05), Culbertson County (65)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 11,590 ± 230 BP ^{14}C
Material: dung
Repository: The Museum, Texas Tech University, Lubbock, Texas
References: Spaulding and Martin (1979), Logan (1983), Harris (1985)

Upper Sloth Cave (Cave 08), Culbertson County (66)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 11,760 ± 610 to 10,750 ± 140 BP ^{14}C
Material: dung
Repository: The Museum, Texas Tech University, Lubbock, Texas
References: Logan and Black (1979), Spaulding and Martin (1979), Harris (1985)

Wheeler, Wheeler County (11)
Identification: *Nothrotheriops texanus* (type)
Age/Date: Irvingtonian II

Material: skeletal
Repository: National Museum of Natural History, Washington, D.C.
References: Hay (1916), McDonald (1995)

Williams Cave, Culbertson County (67)
Identification: *Nothrotheriops* sp.
Age/Date: late Rancholabrean II, 12,100 ± 240 to 11,140 ± 320 BP ^{14}C
Material: skeletal, dung
Repository: Academy of Natural Sciences, Philadelphia, Pennsylvania
References: Spaulding and Martin (1979), Kurtén and Anderson (1980), Harris (1985), Martin et al. (1985)

UTAH

Bechan Cave, Kane County (68)
Identification: *Nothrotheriops shastensis*
Age/Date: late Rancholabrean II, 13,505 ± 580 to 11,630 ± 150 BP ^{14}C
Material: dung, hair
Repository: Laboratory of Quaternary Paleontology, Northern Arizona University, Flagstaff, Arizona
References: Davis et al. (1984), Agenbroad and Mead (1987), Mead and Agenbroad (1992), Jefferson et al. (1994)

Cowboy Cave, Wayne County (69)
Identification: *Nothrotheriops* cf. *N. shastensis*
Age/Date: late Rancholabrean II, 13,040 ± 440 to 11,020 ± 100 BP ^{14}C
Material: dung
Repository: Utah State Museum, Salt Lake City, Utah
References: Hansen (1980), Meltzer and Mead (1985), Agenbroad and Mead (1987), Mead and Agenbroad (1992), Jefferson et al. (1994), F. DeCourten (personal communication, 1995)

Appendix 2 Reported occurrences of *Nothrotheriops* shown to be spurious or suspect.

ALBERTA, CANADA

Medicine Hat
Reported by: Stalker and Churcher (1972)
Status: *Nothrotheriops* sp. or *Megalonyx* sp., assigned to different taxa (Akersten and McDonald, 1991)

ARIZONA

Coconino Cavern, Coconino County (12)
Although cited as *Nothrotheriops* in Lindsay and Tessman (1974), McDonald (1985), and Harris (1985), a careful examination of the material by H.G.M. indicates that the specimen is a single individual of a juvenile *Megalonyx*.

Stanton Cave, Coconino County
Reported by: Lindsay and Tessman (1974)
Status: occurrence disclaimed (J. Mead, personal communication, 1991)

CALIFORNIA

Temecula Arkose, Riverside County
Reported by: Golz et al. (1974)
Status: The single tooth was identified as *Megalonyx* (Akersten and McDonald, 1991)

IDAHO

Castle Creek, Owyhee County
Reported by: Hay (1927)
Status: herein assigned to *Megalonyx leptostomus*

Little Valley, Owyhee County
Reported by: Hay (1927)
Status: herein assigned to *Megalonyx leptostomus*

Wilson Butte Cave, Jerome County
Reported by: Gruhn (1961)
Status: specimen identified as camelid by H.G. McDonald

KANSAS

Adams, Mead County
Reported by: McDonald (1995)
Status: typographic error (H.G. McDonald, personal communication, 1996)

NEVADA

Ladder Cave, White Pine County
Reported by: Graham and Mead (1987)
Status: report in error (J. Mead, personal communication, 1992)

NEW MEXICO

Manzano Cave, Sandoval County
Reported by: Hibben (1941)
Status: identification questionable (W. Bliss, personal communication, 1991), voucher specimen not located

OREGON

Champoeg, Clackamas County
Reported by: TAXIR, Museum of Paleontology University of California, Berkeley
Status: identified as *Megalonyx* sp. (Packard 1952)

UTAH

Shrubox Alcove, Kane County
Reported by: Mead and Agenbroad (1987)
Status: report in error (J. Mead, personal communication, 1992)

Preliminary report of Pleistocene mammals from the state of Coahuila, Mexico

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ABSTRACT. Very little information has been published about Pleistocene vertebrates from the state of Coahuila, Mexico. In this paper, we present the first preliminary report of relatively numerous discoveries of such animals from this state. With the exception of fossil turtle bones at a single site, all known Pleistocene vertebrate finds to date have been of mammals. Most sites have yielded only one or two species, but sites at Rancho Buena Fe (near Parras de la Fuente) and at San Juan de la Vaquería have each produced several species. Most species are documented here for the first time from anywhere in Coahuila. The two localities above are still being investigated, with additional species expected. A total of 12 species are here identified from both, but with only three in common between them: *Mammuthus columbi*; *Camelops* sp., cf. *Camelops hesternus*; and *Equus* sp., cf. *Equus conversidens*. *Equus ?excelsus* possibly occurs at the Rancho Buena Fe locality. Most, if not all, sites in Coahuila listed here are Rancholabrean in age, as determined by the species represented and by radiocarbon dating. However, a prime index fossil for this age, *Bison*, is conspicuously absent from known localities. Two species each of horses and camels, in addition to the mammoth, suggest widespread grasslands. Other taxa, especially deer and mastodon, indicate the presence of woodlands in Coahuila during late Pleistocene time as well.

RESUMEN. Muy poca información han sido publicada sobre los vertebrados Pleistocénicos del Estado de Coahuila, México. Este artículo presenta el primer reporte preliminar de relativamente numerosos descubrimientos de estos animales en dicho Estado. Con la excepción de fósiles de huesos de tortuga en un solo lugar, todos los descubrimientos de vertebrados Pleistocénicos a la fecha han sido de mamíferos. En la mayoría de los sitios hay solamente dos especies, pero en otros, como Rancho Buena Fe (cerca de Parras de la Fuente), y San Juan de la Vaquería, la diversidad es mayor. La mayoría de ellos está siendo documentada por primera vez para Coahuila en este artículo. Las dos localidades arriba mencionadas continúan siendo investigadas con la finalidad de encontrar otras especies. Entre las dos localidades han sido identificadas en total 12 especies, solo tres de ellas en común: *Mammuthus colombi*; *Camelops* sp., cf. *Camelops hesternus*; y *Equus* sp., cf. *Equus conversidens*. *Equus ?excelsus* posiblemente estuvo en la localidad de Rancho Buena Fe. La mayoría si no todos los sitios en Coahuila enlistados aqui, son de edad Rancholabreana, como lo determinan las especies representadas y la datacíon de radiocarbono. Sin embargo, un primer índice de esta edad, *Bison*, está notablemente ausente en las localidades conocidas. Dos especies de caballos y dos de camellos, además del mamut, sugieren pastizales extensos. Otros taxa, epecialmente venado y mastodonte, indican también la presencia de bosques en Coahuila durante el Pleistoceno tardío.

INTRODUCTION

Reports of Pleistocene vertebrates from the State of Coahuila in northeastern Mexico are extremely rare. A brief mention of *Equus* Linnaeus, 1758, and *Elephas* Linnaeus, 1758 (= *Mammuthus* Burnett, 1830) was made by Furlong (1925) on

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the basis of fragmentary material from the vicinity of San Juan de la Vaquería. Even more brief comments were given by Arellano (1951) about the occurrence of *Elephas* (= *Mammuthus*) teeth found near El Durazno. Figure 1 shows the geographic relationship of these two localities in addition to the other sites that are mentioned in this paper.

Most Pleistocene vertebrates recovered in Mexico have come from the State of Mexico, largely because this is where the majority of this country's population lives, and this is also where excavating activities have been focused. The history of late Cenozoic vertebrate discoveries in central Mexico was related by Miller and Carranza-Castañeda (1984). Work on Pleistocene vertebrates in the State of Mexico has proliferated in recent years (e.g., García-Bárcena, 1989; Carballal-Staedtler, 1997; Morett et al., 1998; Polaco et al., 1998; Carbajal-Correa et al., 1999; Pichardo, 2001). However, knowledge of Pleistocene vertebrate sites that produce abundant species is relatively meager for other areas in Mexico. Notable exceptions are productive deposits at El Golfo de Santa Clara in Sonora (Shaw, 1981), San Josecito Cave in Nuevo León (Stock, 1943; Arroyo-Cabrales and Johnson, 1995), Lake Chapala in Jalisco (Rufolo, 1998), Cedazo in Aguascalientes (Mooser and Dalquest, 1975), and possibly Jimenez Cave in Chihuahua (Messing, 1986). Other sites yielding Pleistocene vertebrates in Mexico have been reported, but such reports are relatively uncommon, and they usually relate to very few species. Therefore, any additions to the overall fauna of this age in Mexico are important because they will lead to increased knowledge about geographic range extensions, corridors of dispersal, environmental changes, discoveries of new species, and the possible timing of extinctions of some species. Mexico, with its southern location on the North American continent, might have served as a refugium for some Pleistocene taxa that survived into Holocene time.

Even though the new discoveries of Pleistocene mammals from Coahuila are modest in number (Table 1), they do indicate a high potential for further discoveries in various areas of the state, and additional discoveries came to our attention even as this paper was being completed. It is surprising that *Bison* Hamilton-Smith, 1827, was not found at any locality discussed herein. Also conspicuous by their absence are any South American immigrants.

The construction in 1999 of the Museo del Desierto in Saltillo, the capitol city of Coahuila, Mexico, was a major reason that many Pleistocene mammals became available for study. This new natural history museum is the largest of its kind in Mexico, and it has a strong paleontology program. The Museo del Desierto has become a focal point for people wanting to know more about paleontology. As a result, many people have brought specimens in for identification and have either loaned or donated specimens to the museum, as well as indicated the location of fossil sites. The museum's aggressive program undoubtedly will lead to a rapid accumulation of fossils and to opportunities for their study.

METHODS AND MATERIALS

The vast majority of the fossils that are listed and described in this paper are curated and cataloged in the Museo del Desierto. Specimen and locality numbers are preceded by the museum's paleontology division initials SEPCCP (Secretaría de Educación Pública de Coahuila, Colección Paleontológica). Locality and specimen data for the items listed in this article are on file in the museum. Some of the fossils discussed here were lent by individuals who collected or otherwise have possession of them. In one instance, specimens reported here were made available by an amateur organization from the city of Sabinas known as PASAC (Paleontologos Affeciónados de Sabinas, Asociación Civil). This group has an affiliation with a small museum in Sabinas, the Museo Nacional del Carbón. Members of PASAC have collected fossils in the Sabinas region and have made them available for our inspection. We include in this paper their Pleistocene mammals from the Sabinas locality.

The mammalian classification used in this paper follows Kurtén and Anderson (1980) in many, but not all, aspects. It also conforms to usage by other investigators (e.g., Lundelius et al., 1987; Dalquest and Schultz, 1992; Arroyo-Cabrales and Johnson, 1995). Habitats given for genera and species discussed come from Miller (1971), Kurtén and Anderson (1980), Hall (1981), and Dalquest and Schultz (1992). It is also assumed that past climatic tolerances and possible habitats of extinct species closely approximate those of their living counterparts. Specimens identified in this work were compared with both fossil and Recent material in the Brigham Young University collections and the Natural History Museum of Los Angeles County.

Unless otherwise indicated, all reported measurements are in millimeters. Lamellar frequency (LF) and enamel thickness (ET) measurements of mammoth teeth were taken in accordance with those recommended by Lister (2002). Measurements shown in parentheses indicate approximations.

ABBREVIATIONS

NALMA	North American Land Mammal Age
BYU	Brigham Young University, Provo, Utah USA

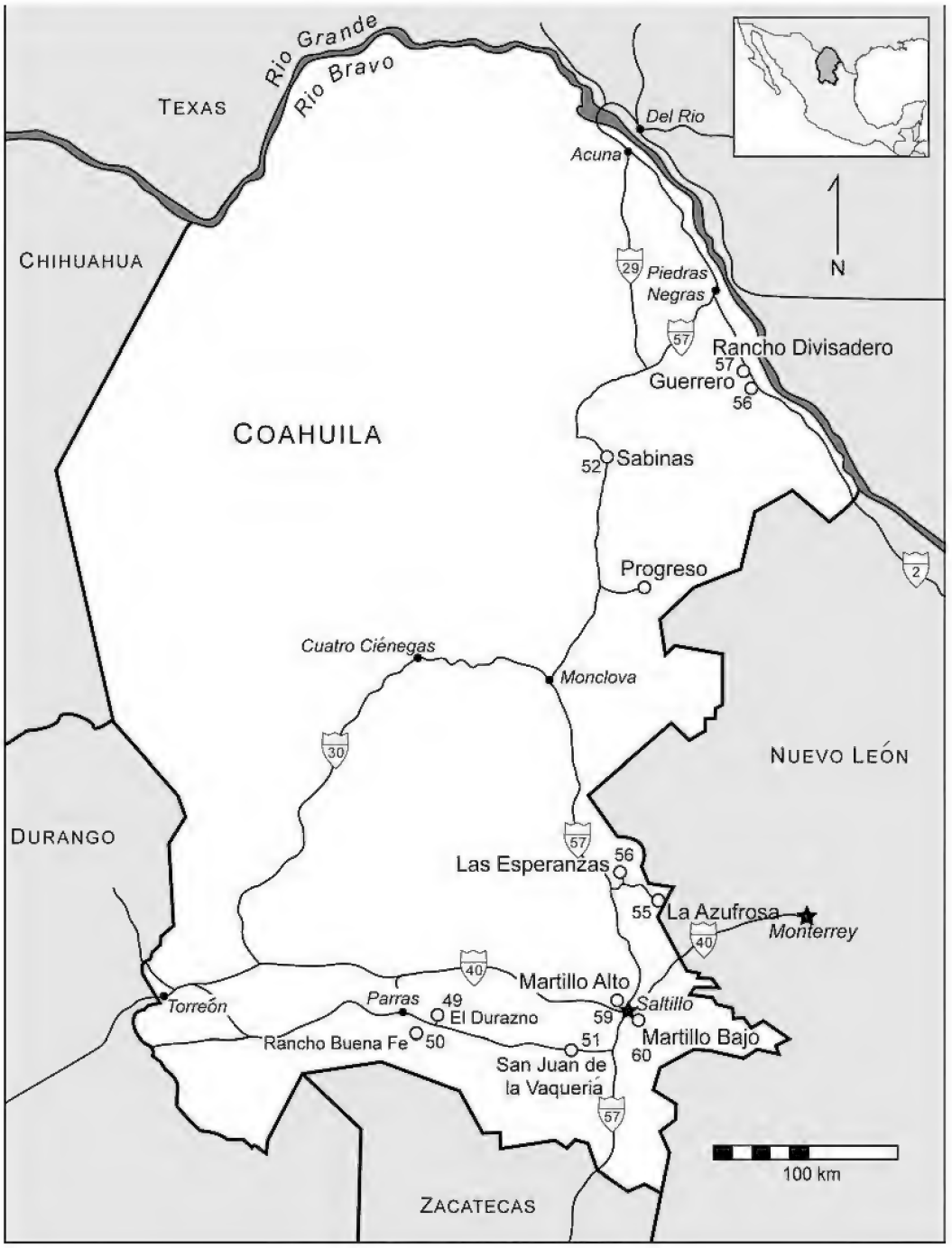

Figure 1 Index map showing late Pleistocene fossil localities in Coahuila, Mexico.

INAH Instituto Nacional de Antropología e Historia, México

LACM Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California USA

UCR Department of Geological Sciences, University of California, Riverside, California; collections and records now maintained at the Museum of Paleontology, University of California, Berkeley, California USA

Table 1 Faunal list of Pleistocene mammals from Coahuila, Mexico. **ABBREVIATIONS: ED** = El Durazno; **RBF** = Rancho Buena Fe; **SJV** = San Juan de la Vaquería; **P** = Progreso; **S** = Sabinas; **LA** = La Azufrosa; **G** = Guerrero; **RD** = Rancho Divisidero; **LE** = La Esperanza; **MA** = Martillo Alto; **MB** = Martillo Bajo.

	Locality										
Taxon	ED	RBF	SJV	P	S	LA	G	RD	LE	MA	MB
Silvilagus ?leonensis		X									
cf. *Lepus*		X									
Pappogeomys cf. *castanops*		X									
Canis cf. *latrans*		X									
Mammut americanum			X	X		X					
Mammuthus columbi	X	X	X	X	X	X	X	X	X	X	X
Equus cf. *conversidens*		X	X		X						
Equus ?excelsus	X	X	X		X						
Camelops cf. *hesternus*	X	X	X		X						
Hemiauchenia cf. *macrocephala*			X								
Odocoileus ?virginianus		X									
Capromeryx cf. *mexicana*			X								

All fossil localities discussed appear in Figure 1. Most of the material described in this paper was collected between 1999 and 2003. Standard practices were employed in fossil collection. Screening operations to date have been minimal, but this essential collecting technique will be increased during future field work. Although a number of radiocarbon dates were attempted by Beta Analytic, Inc., of Miami, Florida, and the Radiocarbon Laboratory at the University of California, Riverside, only those based on wood are reliable.

GENERAL GEOLOGY

OVERVIEW

The State of Coahuila lies mostly within the Sierra Madre Oriental province of eastern Mexico. This province was created by a Laramide age fold and thrust belt that trends essentially in a northwest–southeast direction in the northern portion of the state but in an east–west orientation in the southern part. A series of basins was produced both between and within these ranges. The two most dominant basins are the east–west trending Parras Basin in southern Coahuila (McBride, 1974; McBride et al., 1975) and the northwest–southeast directed Sabinas Basin in the northern part of the state (Goldhammer and Johnson, 1999). Most ranges of the Sierra Madre Oriental in the state expose Upper Cretaceous sedimentary rocks that vary from conglomerates through limestones (Instituto Nacional de Estadistica, Geografia e Informatica, 1981). Sandstones, shales, and limestones are the dominant Cretaceous lithic types that we have observed in many areas throughout the state. Interbedded marine and nonmarine beds contain locally abundant fossils, including dinosaurs. Most of the dinosaurs that have been collected in Mexico came from Coahuila, and many of these are currently under study. Older reports exist in which these unique vertebrates from the state are mentioned (e.g., Janensch, 1926; Murray et al., 1960; Rodriguez-De La Rosa and Cevallos-Ferriz, 1998). In some areas, such as around the village of Progreso (Fig. 1), coal beds occur in Upper Cretaceous strata.

Many small basins exist both within and without the two major basins mentioned above. In all cases with which we are familiar, these small basins contain relatively thick deposits of Quaternary age sediments. In some areas, these are mostly Pleistocene in age, and in others, they are Holocene. Although numerous areas were examined by the authors of this article, no Tertiary age sediments were found. Sediments examined were all clastic in nature and range from coarse gravels through clays and muds. Collected fossils came from all these lithologies, but most were found in sands, silts, clays, and muds.

FOSSIL LOCALITIES

El Durazno (SEPCCP 49)

This is one of the two vertebrate fossil sites in the state of Coahuila that have been previously mentioned in the literature (Fig. 2). Only an identification of elephantid teeth was given (Arellano, 1951). A large arroyo extends through the village of El Durazno where other fossils were discovered. Walls of the arroyo vary in height, but they usually extend from 8 to 9 m above the arroyo floor. Two disconformities are present, with the few fossils from this locality having been derived from beneath the lower one, which undulates at 2 or 3 m above the base of the arroyo. A thin gravel layer occurs above this disconformity, and a unit of mixed brownish gray, silty mudstone occurs beneath it. The fossils that have been collected

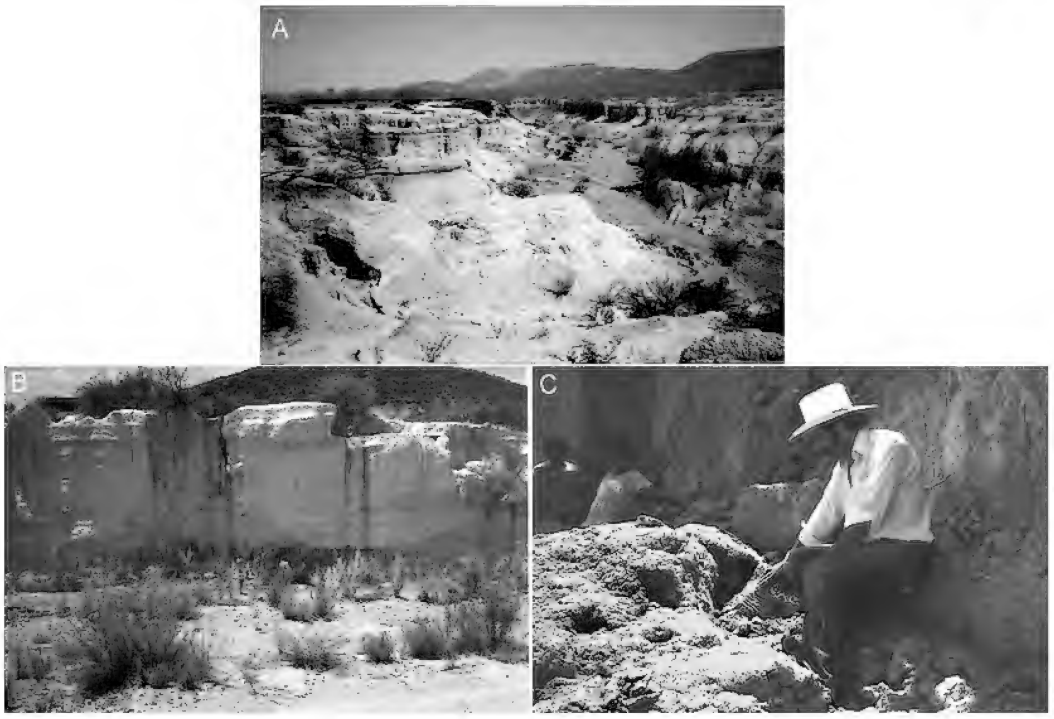

Figure 2 The El Durazno fossil locality: **A,** the general locality area; **B,** specific area of fossil recovery; **C,** Celso Pérez, discoverer of *Camelops* teeth, pointing out mammoth tooth *in situ*.

here came from the lowest unit. A Beta Analytic, Inc., $^{13}C/^{12}C$ age based on wood is 41,150 BP (Beta sample 151834). Elevation 1,520 m.

Rancho Buena Fe (SEPCCP 50)

Located in farmland approximately 4 km east of the city of Parras de la Fuente (Fig. 3), the locality is an abortive well that was dug in April 2000. In the process of the excavation, fossils were uncovered at a depth of 7 to 8 m. Mostly fine-grained sediments exist through the 8-m section. Fossils were found near the base of this well hole in dark brown muds and clays. Much fossil woody material was found, partly matted, associated with abundant freshwater snails and the vertebrate fossils. A University of California, Riverside, $^{13}C/^{12}C$ age based on some of the wood from this deposit is 11,740 ± 50 BP (UCR sample 3866). Elevation 1,530 m.

San Juan de la Vaquería (SEPCCP 51)

Furlong (1925) indicated that fragmentary bones and teeth of horse and mammoth were discovered near this village. It is not known whether these came from the restricted area that we have designated as the San Juan de la Vaquería locality (Fig. 4), but Furlong's locality apparently was close to it. Potential fossil-bearing sediments occur for some distance outside the village, and these will be examined later in more detail. Our locality measures approximately 20 by 50 m, and it is on the outskirts of the village adjacent to the town soccer field. Most of the fossils collected here were discovered in a shallow arroyo, about 2 m at its greatest depth. Fossils mostly derive from greenish brown muds and clays and fine-grained, tan sands. Pebble-sized to small cobble-sized clasts exist throughout the exposed finer grained sediments. This site is unusual because almost all of the recovered fossils are teeth, including tusks. Elevation 1,840 m.

La Azufrosa (SEPCCP 55)

In 1999, an excavation was made to expand a spa that had been built on some geothermal hot springs in this village. Bones of a single individual mastodon were uncovered during this excavation. It was reported that this find was made at approximately 3 m below the surface. Sediment still adhering to the fossils is a gray clayey silt, and this matches sediment at the 3 m depth in other nearby exposures. The overlying beds, however, are mostly composed of coarser material: sands and gravels that contain cobbles and small boulders. These deposits apparently represent alluvial material that was washed in from the

Figure 3 Rancho Buena Fe fossil locality: **A,** area of well site yielding fossils (people grouped around well hole); **B,** close-up view of well hole after rains filled it in following initial fossil recovery; **C,** reexcavation of the well site.

highlands that are immediately to the east of the village. A water-worn mammoth tooth was also recovered at a depth of 1.5 m in the same vicinity. Elevation 770 m.

Guerrero (SEPCCP 56)

This site is approximately 5 km south-southeast of the town of Guerrero. Mammoth teeth found here reportedly came from near the surface in thin beds of sand and gravel that unconformably overlie fossiliferous Upper Cretaceous green-colored marine siltstones and shales. Ammonites, clams, and burrow structures are present in the Cretaceous strata. Elevation 220 m.

Rancho Divisadero (SEPCCP 57)

Located about 3 km northwest of the Guerrero site, near Arroyo Paloblancos, a tusk and bone fragments (presumably of mammoth) were found in low hilly terrain. These fossils occurred at the surface in a grayish sandy silt. Elevation 200 m.

Las Esperanzas (SEPCCP 58)

The locality is in Arroyo Piedritas, approximately 1 km north of the village of Las Esperanzas. An M3 of *Mammuthus* was collected at this locality by local inhabitants, who also reported other

Figure 4 The San Juan de la Vaquería fossil locality showing part of main fossil-producing arroyo.

mammoth bones in the area, which we could not locate, however. Elevation 870 m.

Arroyo El Martillo Alto (SEPCCP 59)

This site is in a major arroyo, extending through the east side of the city of Saltillo, that is generally oriented north–south. Sand and gravel deposits of Pleistocene age rest unconformably on Upper Cretaceous shales. Walls of this arroyo are 3 to 4 m in height. Mammoth cranial material, including a tooth, was found in gravelly sediments that are exposed in the side of the arroyo at approximately 2 m above the arroyo floor. Elevation 1,580 m.

Arroyo El Martillo Bajo (SEPCCP 60)

This locality is approximately 4 km north of the previously mentioned locality, Arroyo El Martillo Alto, and is in the same water course. The geologic situation that was noted for the latter locality is the same here. Mammoth teeth and tusk fragments were collected at this site, but these are no longer available for study. Elevation 1,510 m.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Lagomorpha Brandt, 1855

Family Leporidae Gray, 1821

Sylvilagus Gray, 1867

Sylvilagus ?leonensis Cushing, 1945

Sylvilagus leonensis Cushing, 1945:183–184.

REFERRED SPECIMENS. Proximal half of a right femur, distal four fifths of a right tibia–fibula, and left tibia–fibula fragment of one individual (SEPCCP 341) from Rancho Buena Fe.

DISCUSSION. Many genera and species of Pleistocene lagomorphs are known from North America. They have been reported from numerous localities, from Alaska to Mexico. The most abundant finds are of the genera *Lepus* Linnaeus, 1758, and *Sylvilagus* Gray, 1867, which include most of the common extant North American leporid species. Species identifications of fossil lagomorphs usually are made on the basis of the lower third premolar. Although no dentition was found at Rancho Buena Fe, the size of the limb bones indicates a pygmy rabbit. They are, however, larger than the pika, *Ochotona* Link, 1795. According to Burt and Grossenheider (1964), *Sylvilagus idahoensis* (Merriam, 1891) is the smallest living North American rabbit, and it can be distinguished from all other extant forms on the basis of size alone. Hall (1981) has shown that the distribution of this species is restricted to the northwestern part of the United States. In a comparison with femora and tibiae–fibulae that have been identified as *Sylvilagus* sp., cf. *S.*

idahoensis, from the Silver Creek Local Fauna in Utah (Miller, 1976), the Rancho Buena Fe fossils are identical in size, and their morphologies show only minute differences. The extinct pygmy rabbit from San Josecito Cave in Nuevo León, Mexico, *S. leonensis* Cushing, 1945, is similar in size to *S. idahoensis*, but it possesses a wider palate, upper molariform teeth that have crenulate external reentrant angles, and a p3 with a broad shallow reentrant angle that is not present in the Idaho rabbit. However, without dental material available for the Rancho Buena Fe rabbit, no positive identification to species can be made.

The present specimens were compared with leporids from San Josecito Cave in the collections of the LACM. Two species are recognized from this site: a larger, unidentified form of *Sylvilagus* and *S. leonensis*. The limb elements from Rancho Buena Fe are identical to comparable elements of the pygmy rabbit from San Josecito Cave. Because Coahuila borders Nuevo León and because no other similar-sized leporids are known of Pleistocene or Holocene age in northeastern Mexico or in the southwestern United States, the present material is questionably referred to *S. leonensis* on the basis of morphological congruency, size, and known geographic occurrences. This is the first report of a Pleistocene rabbit from Coahuila.

INFERRED HABITAT. Presumably brushy and wooded terrain.

Lepus Linnaeus, 1758
cf. *Lepus* sp.

Lepus Linnaeus, 1758:57.

REFERRED SPECIMENS. Incomplete right and left innominate bones (SEPCCP 342) from Rancho Buena Fe.

DISCUSSION. The pelvic bones of a large leporid were recovered in association with the smaller rabbit specimens at Rancho Buena Fe. They are considerably larger than any species of *Sylvilagus* that is known from the region, either Pleistocene or Holocene. Although it is not advisable to refer these specimens to any species, they compare most favorably to the genus *Lepus*. These pelvic bones are identical in size and shape to corresponding ones of *Lepus californicus* Gray, 1837, the blacktail jackrabbit. This species is present in Pleistocene age deposits of Mexico, and it occurs throughout the state of Coahuila today.

INFERRED HABITAT. Varied, but commonly brushy areas including deserts and temperate regions.

Order Rodentia Bowdich, 1821
Family Geomyidae Bonaparte, 1845
Pappogeomys cf. *P. castanops* (Baird, 1852)

Pseudostoma castanops Baird, 1852, appendix C:313.

REFERRED SPECIMENS. Horizontal ramus of a left dentary with complete incisor, P4 and broken m1 (SEPCC3eP 343) and an isolated incisor (SEPCCP 344) from Rancho Buena Fe.

DISCUSSION. Gophers commonly occur as Pleistocene fossils throughout the continental United States and, to a lesser extent, in Mexico. They are less common in Canada, especially in the northern regions. Gophers are moderately diverse in genera, very diverse in species. Fewer fossil forms are known from Mexico, and this is apparently a result of fewer Pleistocene vertebrates having been reported from that country, where few fossil-producing sites have been screened for microvertebrates. However, those sites showing at least modest taxonomic diversity usually yield at least one species of gopher. Hibbard (1955) reported *Thomomys* sp. and *Cratogeomys* sp., cf. *C. tylorhinus* (Merriam, 1895), from the Valley of Tequixquiac. Russell (1960) recognized *Thomomys umbrinus* (Richardson, 1829), *Cratogeomys castanops* (Baird, 1852), *Cratogeomys* sp., and a new species of *Heterogeomys, H. onerosus* (Russell, 1960), and Mooser and Dalquest (1975) have identified two species from the Cedazo Local Fauna at Aguascalientes (?*T. umbrinus* and *Pappogeomys* cf. *P. castanops*). Currently, there is disagreement as to whether *Pappogeomys* Merriam, 1895, and *Cratogeomys* Merriam, 1895, should be considered separate genera. We chose to follow Hall (1981:517) in regarding *Cratogeomys* as a subgenus of *Pappogeomys*.

The horizontal ramus of the dentary of the gopher from Rancho Buena Fe has a diastem length from the incisor to p4 of 10.4, a least depth of the diastem of 5.8, and a 9.5 depth of dentary beneath the p4. Transverse width of the incisor in this dentary is 2.6, and that for the isolated incisor is 2.8. Much smaller size alone separates this gopher from the specimens of *Heterogeomys* Merriam, 1895, from San Jocecito Cave. Arroyo-Cabrales and Johnson (1995) refer to the genus as *Orthogeomys* Merriam, 1895. The mandible we report from Coahuila, with its p4, differs from species of *Thomomys* Wied-Newwied, 1839, in its much larger and well-rounded trigonid, as opposed to a small angular one. The trigonid–talonid isthmus is relatively long in the present specimen. The m1 (broken at the alveolar border) has a much more transversely elongate diameter than is typical of a similar-sized species of *Geomys* (Rafinesque, 1817). On the p4, the trigonid of the Coahuila specimen has a rounded anterior surface of the trigonid rather than a pointed one, as is present in specimens of *Geomys*. Also, the incisors of the two Mexican specimens show

much less curvature. In a comparison with *P. castanops*, the Rancho Buena Fe material could not be distinguished from it. For this reason, it seems referable to this species. This species is found living in the state of Coahuila today, and it is known as the Mexican, or yellow-faced, pocket gopher.

INFERRED HABITAT. Fossorial for gophers in general, with an apparent preference for sandy soils.

Order Carnivora Bowdich, 1821

Family Canidae Gray, 1821

Canis cf. *C. latrans* Say, 1823

Canis latrans Say, 1823:168.

REFERRED SPECIMENS. Complete third cervical vertebra (SEPCCP 345) and major portion of a left femur (SEPCCP 346) from Rancho Buena Fe.

DISCUSSION. Coyotes are among the most widespread and abundant members of the order Carnivora in Pleistocene deposits of North America. Today, they range over most of the continent, from Alaska to southern Central America, and apparently they did so in the past. However, they have been reported from only a few sites in Mexico, and never before from Coahuila. It has long been thought that the living coyote was a direct descendant of *Canis lepophagus* Johnston, 1938, of the Blancan North American Land Mammal Age (NALMA). A geochronologically earlier coyote species, *Canis ferox* Miller and Carranza-Castañeda, 1998, is considered to be ancestral to *C. lepophagus*. *Canis ferox* is thought to be the earliest form of *Canis* yet discovered, and it is from Hemphillian age deposits in Guanajuato, Mexico.

The canid bones from Rancho Buena Fe were compared with similar elements of many modern coyotes, and they were found to fall within the range of size and morphologic variability of *C. latrans*. The fossils were also compared with corresponding bones of *C. latrans* from San Josecito Cave (in LACM), from which they are indistinguishable. In greatest diameter, the femoral head of SEPCCP 346 measures 18.1 mm (the shaft of this bone lacks the distal end). The third cervical vertebra (SEPCCP 345) is 36.4 mm in greatest anteroposterior length, 31.1 mm in transverse width, and 29.8 mm in greatest anteroposterior length of the centrum. Mooser and Dalquest (1975) named *Canis cedazoensis* from Pleistocene deposits near the city of Aguascalientes in central Mexico. This species was reportedly larger than the largest of North American foxes, but smaller than *C. latrans*. Apparently this small dog has not been recognized subsequently at any other locality, and according to Kurtén and Anderson (1980), the relationship of *C. cedazoensis* to other known canids is unresolved. In their discussion, Mooser and Dalquest (1975) indicated that the holotype, a maxillary fragment with P3–M1 and alveolus for M2, was originally accompanied by a more complete specimen, which was lost and was not described. The protocone on the P4 of the holotype was said to be missing. Considering the size variation among fossil and Holocene coyotes, and the very limited material representing the holotype and only specimen, the validity of this species should be regarded as questionable.

INFERRED HABITAT. Coyotes are found in a variety of habitats throughout most of North America.

Order Proboscidea Illiger, 1811

Family Mammutidae Cabrera, 1929

Mammut americanum (Kerr, 1792)

Elephas americanus Kerr, 1792:116.

REFERRED SPECIMENS. Partial right and left premaxillae, both maxillae and dentaries with dentitions, basicranium, axis vertebra, and right ulna from La Azufrosa (SEPCCP 370, Fig. 5). Right and left m1 and left dp4 of a juvenile from Progreso (SEPCCP 371, Fig. 6), and a left m2 from San Juan de la Vaquería (SEPCCP 290).

DISCUSSION. It is generally accepted that *M. americanum* is the only Pleistocene species of the genus in North America (King and Saunders, 1984). It was abundant during Pleistocene time in eastern North America and is documented by abundant fossils there, but much less abundant in the more arid western parts of North America. Although Kurtén and Anderson (1980) indicated a geographic distribution from Alaska to Florida, a few discoveries have been reported from Mexico as far south as the Yucatán Peninsula and Chiapas (Osborn, 1942; Miller, 1987; Polaco et al., 1998; Pichardo, 2001). García-Bárcena (1989) stated that the Yucatán occurrence was in the Loltún Cave deposits, but Arroyo-Cabrales and Alvarez (2003) listed the only proboscidean from this site as an unidentified species of *Cuvieronius* Osborn, 1923. Pichardo (2001) reported a specimen from the Valsequillo area of central Mexico. That mastodon was associated with human artifacts, indicating a kill site. The reports herein of *M. americanum* from three widely separated areas in Coahuila add significantly to knowledge of this species in Mexico.

Dalquest and Schultz (1992) stated that this species was extremely rare in northwestern Texas and that prairie and grassland habitats were apparently not suitable for it. García-Bárcena (1989) indicated that during the Pleistocene, *M. americanum* probably followed a corridor into Mexico along the eastern margin of the Sierra Madre Occidental. Although this route is possible, the present finds indicate that a more

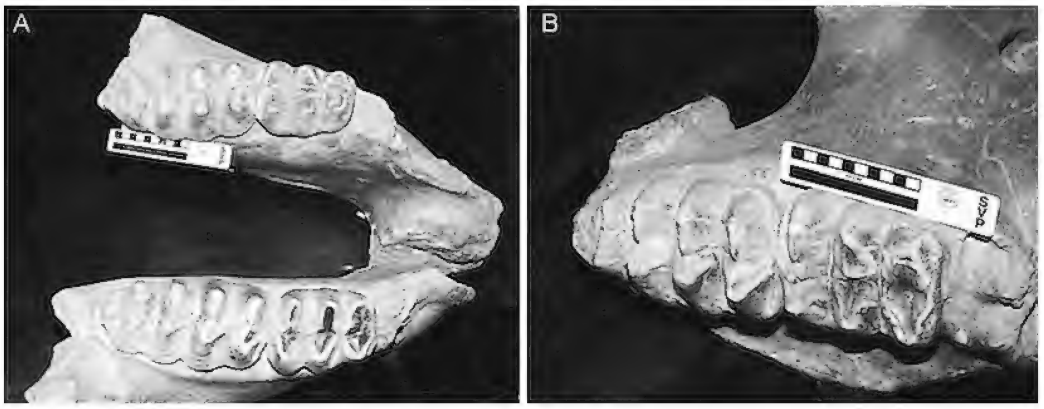

Figure 5 *Mammut americanum* (Kerr, 1792), the mastodon from La Azufrosa on display at the Museo del Desierto, Coahuila: **A,** close-up of mandible; **B,** close-up of right maxilla. Scale bars = 10 cm.

probable route was along the western margin of the Sierra Madre Oriental, as well as possibly through these mountains. With American mastodons reported occurring at an elevation of approximately 3,000 m in Utah (Miller, 1987), and from a site in New Mexico at an elevation of more than 2,000 m (Lucas and Morgan, 1997), it seems plausible that this species could have dispersed through high mountain terrains. The few previous discoveries of this species in Mexico came from localities that are situated on the Mexican Highlands at reported elevations above 1,500 m (Polaco et al., 1998). However, only one of the three mastodon localities in Coahuila, the one at San Juan de la Vaquería, is at an elevation that is higher than this, at 1,840 m.

The mastodon from La Azufrosa came from an elevation of 770 m, whereas the juvenile from Progreso was found at the lowest elevation among these records, at approximately 300 m. The two latter finds are much lower in elevation than any previously reported mastodons from Mexico. It is posited that woodlands, including riparian habitats, existed near where these animals were living. Although radiometric dates have not yet been obtained for the present specimens, Van Devender and Bradley (1990) indicated that during the late Wisconsin age, woodlands existed at lower elevations than today in the Bolsón de Mapimí area of central and east Coahuila. This area, which lies between the Sierra Madre Oriental and Sierra Madre Occidental, has elevations lower than 1,000 m. A variety of specific habitats undoubtedly existed in Coahuila during the Pleistocene, but based on current knowledge of the proboscideans from Coahuila (*Mammut* and *Mammuthus*), those habitats that were favorable for the mammoths must have predominated. This is based on the greater number of specimens and more widespread localities for the mammoth. This appears to be true, despite the mastodon being considered more of a generalist feeder than the mammoth (Shoshani, 1989).

Figure 6 *Mammut americanum* (Kerr, 1792), the mastodon from Progreso; occlusal views of right and left m1.

Among the three sites that yielded American mastodon in Coahuila, La Azufrosa produced the best material. As reported above, this individual was found associated with hot springs. It is possible that the animal was trapped in soft sediments there, and that its preservation was enhanced by quick burial. The sands at this site, especially when wet, appear conducive for this situation. Incomplete as it is, this material probably represents the most complete individual of any Pleistocene mastodon from Mexico, especially with regard to dentition. The preserved skull parts consist of a large portion of the basicranium with the right and left premaxillae, maxillae, and dentaries with their second and third molars (Fig. 5). Additionally, an axis vertebra and right ulna were recovered. Dental measurements of this specimen appear in Table 2. Because this seemingly is the most complete

Table 2 Dental measurements of *Mammut americanum* from La Azufrosa (private collection), Progreso (private collection), and San Juan de la Vaquería (SEPCCP 290), Coahuila, Mexico. All measurements are in millimeters; those in parentheses are approximate.

	Maximum length	Maximum width	Widest loph/lophid
La Azufrosa specimen			
Right M3	177	106	Second
Left M3	177	104	Second
Right m3	192	109	Second
Left m3	190	110	Second
Right M2	123	103	Third
Left M2	123	98	Third
Right m2	117	97	Second
Left m2	118	100	Second
Progreso specimen			
Left dp4	58	38	Third
Right m1	88	52	Third
Left m1	90	53	Third
San Juan de la Vaquería specimen SEPCCP 290			
Left m2	115	(85)	Third

representation of the American mastodon dentition from Mexico, details are provided with its description.

Preservation of the present material is generally very good. Shallow alveoli for both the right and left M1 suggest that these teeth had been shed before the animal died. Enamel on M2 and M3 lophs shows some plications, and these teeth conform more closely with the smooth-toothed variant, rather than the rough variant of the American mastodon. Such differences among molars of the American mastodon were first reported by Leidy (1869), and they have been subsequently referred to by others (e.g., Saunders, 1977; Miller, 1987). This variation in the rugosity of the molar enamel has been considered to be diet related and not indicative of species differences (Miller, 1987). King and Saunders (1984) suggested that the rugged variant of the molars was an adaptation to pine-dominated vegetation. In the rugose variants, the pattern of enamel rugosities is commonly present only along the sides of the molars, but in some specimens, it extends onto the valley walls of the lophs and lophids.

These conditions are not present in the molars of the mastodon from Azufroza; the valleys of its molars are smooth and unobstructed. Cingula are modestly developed on M2s and M3s, being more pronounced on the latter. Wear is more pronounced on the right side of the dentition, both the upper and the lower. The dentine shows widely contiguous tracks on first M2 lophs, separated tracks on the second loph, with distinct pretrite and posttrite cusps on the third loph. Wear is minimal on the first loph of both M3s, with a small exposure of dentine on the posttrite cusp only on the right M3. The second M3 loph shows very little wear (no dentine exposed), and the third and fourth lophs have none. Tiny conelets appear on these latter unworn lophs. No true pentaloph is present, although an incipient pentaloph occurs on the left M3. A small amount of cementum is present on both M3s, increasing posteriorly on each tooth. The right premaxilla has much of the tusk alveolus still intact. It measures approximately 13 cm in diameter, and the large size of this alveolus indicates that the specimen was a male.

The right and left dentaries each contain an m2, an m3, and a remnant of the m1 alveolus. Although no mandibular tusks are present, nor alveoli for them, small rugose protuberences are present where small tusks might have occurred earlier in the ontogeny of the individual. Kurtén and Anderson (1980) stated that American mastodon males had small vestigial lower tusks that were usually lost by maturity. Only the right dentary has a portion of its ascending ramus preserved.

As with the upper dentition, the lower molars are worn asymmetrically, the right molars having more wear than the left molars. Dentine is widely contiguous on the first and second lophids of the right m2, but it shows enamel separation on the second lophid of the left m2. Dentinal wear is not contiguous on either third lophid of this tooth. On the m3s, dentine shows only on the outside cuspid of the first lophid of both. Very little enamel wear exists on the second lophid of this molar, but the wear is greater on the right m3. The third and fourth lophids of both m3s show no apparent wear. An incipient lophid (pentalophid) is present on each. Smoother surfaced enamel is present on the lower molars compared with the uppers; however, simple plications do appear on the posterior sides of the third and

fourth lophids of both m3s. The valleys between the lophids are all clear.

American mastodon molars vary considerably in size. The greatest lengths and widths of the molars of the mastodon from La Azufrosa are considerably larger than those of mastodons from Utah (Miller, 1987), larger than all but one specimen from New Mexico (where the lengths of m2 and m3 are greater but the widths are less [Lucas, 1987; Lucas and Morgan, 1997]), larger than most specimens from Trolinger Spring, Missouri, but similar to the average from Boney Spring, Missouri (Saunders, 1977), and close to the average size of several specimens from Michigan (Skeels, 1962).

Another site that yielded a mastodon was at San Juan de la Vaquería. An isolated m2 (SEPCCP 290) of an adult animal was found in a fine sandy unit (Table 2).

A juvenile mastodon is represented by an unworn right and left m1 and a partly worn dp4, all from a single individual that was discovered in 1994 during coal mining excavations near the town of El Progreso. It was reported that these teeth were recovered between 3.5 and 4.0 m beneath the surface in a sandy unit. We examined the area of the site (which is now covered over), and observed that Pleistocene deposits unconformably overlie Upper Cretaceous strata. From information that we obtained from persons familiar with the mining operations, about 60 m of Quaternary sediments overlie the coal-bearing Cretaceous rocks. Measurements of this juvenile dentition are in Table 2. These teeth are of the coarse rugosity variant of mastodon, in contrast to the adult teeth from La Azufrosa and San Juan de la Vaquería.

INFERRED HABITAT. Conifer forests and woodlands, including riparian environments and wetlands.

Family Elephantidae Gray, 1821

Mammuthus columbi (Falconer, 1857)

Elephas columbi Falconer, 1857:319.

REFERRED SPECIMENS. Skull fragments, left m3, lumbar vertebra, three ribs, most of right and left femora, fibulae, and a partial calcaneum, apparently from one individual (SEPCCP 297) from Rancho Buena Fe. M1 from La Azufrosa (SEPCCP 377). Partial tusks (SEPCCP 307, 308, 317); complete and incomplete molars (SEPCCP 291–297, 305, 306, 309, 311–316); and scapula and distal end of humerus (SEPCCP 320) from San Juan de la Vaquería. Two partial tusks (SEPCCP 379), an M3 (SEPCCP 380), two partial upper molars (SEPCCP 381 and 382), and a dentary with m2–3 (SEPCCP 323) from the Sabinas region. Two M3s and dentary with m3 from single individual, an m1 and tusk section from Guerrero (specimens from private collection Enrique Cervera). Uncollected tusk, accompanying tooth plate fragments, and uncollected limb bone from Rancho Divisadero. M3 (specimen from private collection of Isauro and Raymundo Mata) and uncollected limb bones from Las Esperanzas. Skull fragments with unavailable molars from El Martillo Alto, and skull fragments and tooth fragments from El Martillo Bajo. Three molars, and two tusk pieces from unknown localities in Coahuila.

DISCUSSION. As has been noted in numerous studies, mammoths first migrated to North America during the Irvingtonian NALMA, and they serve as an index fossil for the Pleistocene (Savage, 1951; Lundelius et al., 1987). Early mammoths passed from Asia through Beringia to the New World, and *Mammuthus meridionalis* (Nesti, 1825) and *Mammuthus hayi* (Barbour, 1915) are considered to represent these early immigrants (Agenbroad, 1984; Madden, 1995). According to Lindsay et al. (1975), mammoths arrived in North America at about 1.5 Ma. Others (e.g., Agenbroad, 1984) extend that date earlier, to 1.8 Ma. No authentic records of mammoth exist for South America.

Confusion exists concerning the distinction of the later Pleistocene species *Mammuthus imperator* and *M. columbi* resulting from inadequate holotypes, which in each case are fragmentary M3s. Leidy (1858a) designated the species, *M. imperator*, but he later opined (Leidy, 1869) that this species was conspecific with Falconer's (1857) *M. columbi*. Osborn (1922) designated neotypes for each species in an attempt to clarify the situation; however, those specimens proved inadequate to distinguish these species. Researchers currently are not in agreement on taxonomic usage (e.g., Kurtén and Anderson, 1980; Lucas et al., 2000; Pichardo, 2001), in that some recognize *M. imperator* as valid and some do not. Presumably, *M. imperator* has fewer and thicker enamel plates on the molars (usually the M3s are used for comparisons) than *M. columbi*. Agenbroad (1984) suggested temporal gradation in species, with plate numbers increasing and enamel thicknesses of plates becoming thinner through the Pleistocene, from *M. meridionalis* to *M. imperator*, to *M. columbi*, to *Mammuthus jeffersoni* (Osborn, 1922), to *Mammuthus primigenius* (Blumenbach, 1799).

However, this scenario is contradicted by the discovery of teeth assignable to two species on the basis of the above criteria at one locality (Miller, 1971), when in all probability only one taxon exists. Miller (1971, 1976) regarded *M. imperator* as conspecific with *M. columbi*. Agenbroad (2003) regarded both *M. jeffersoni* and *M. imperator* to be invalid species, with most of the specimens that have been assigned to them being referable to *M. columbi*. We are in agreement with Agenbroad on this, and we do not recognize

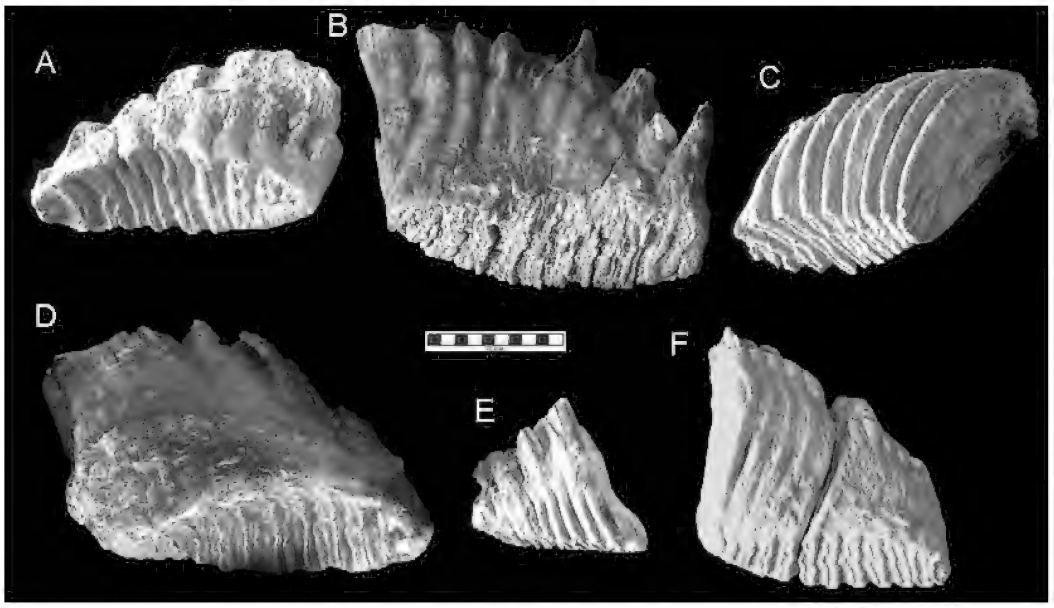

Figure 7 *Mammuthus columbi* (Falconer, 1857), isolated teeth from various localities in Coahuila: **A,** SEPCP 49/331, from El Durazno; **B,** SEPCP 50/297, from Rancho Buena Fe; **C,** SEPCP 51/292, from San Juan de la Vaquería; **D,** SEPCP 62/332, from El Ojuelo; **E,** SEPCP 51/291, from San Juan de la Vaquería; **F,** SEPCP 51/330, from San Juan de la Vaquería. Scale bar = 10 cm.

either *M. imperator* or *M. jeffersoni* as valid species. This differs from Kurtén and Anderson's (1980) classification, wherein both species were considered to be valid.

Mammoths, and in particular *M. columbi*, are arguably the most common Pleistocene vertebrate fossils from Mexico. The first published report of any vertebrate fossil from this country is of a proboscidean, and apparently it was a mammoth (Anonymous, 1799). These animals have been discovered from both northern and southern Mexico, from Sonora (Osborn, 1942; Lucas and González-León, 1996) to Oaxaca (Osborn, 1942). A vast majority of mammoth fossils, some at purported kill sites (Irwin-Williams, 1967), have been recovered in the state of Mexico in the south-central part of the country. This is not surprising, because most human excavating activities in Mexico have taken place there, and it is by far the most populated part of the county.

To date, mammoths definitely constitute the most widespread as well as abundant Pleistocene vertebrate fossils from Coahuila. The earliest scientific report of a mammoth from Coahuila appears to be that by Furlong (1925; as *Elephas*) on the basis of fragmentary teeth and bones that were found near Saltillo. Arellano (1951) also noted elephantid teeth from the area of El Durazno. In our contacts with people in various cities and villages throughout Coahuila, we heard many reports of tusks, teeth, and bones that probably were of mammoth. We examined as many of the reported specimens and sites as possible. Although often the fossils had been destroyed by erosion earlier or were unavailable to view if collected for various reasons, several finds were made available to us (Fig. 7). Also, some teeth and tusk fragments have been given to the Museo del Desierto, but without locality data other than having been found in the state of Coahuila. It seems that all can be ascribed to *M. columbi*. Lamellar frequency averages for both complete and incomplete molars (if greater than 100 mm) on all museum specimens vary from 6.5 to 8.5, with an average of 7.3. Enamel thicknesses of individual plates vary from 2.0 to 3.1 mm, with an average of 2.4 mm.

The most complete individual mammoth specimen from Coahuila was recovered from the well site at Rancho Buena Fe near the city of Parras de la Fuente. It was collected at a depth of approximately 8 m. Skeletal elements of this individual consist of skull parts, a left m3 (Fig. 8), a partial pelvis, three ribs, a lumbar vertebra, large portions of the left and right femora, a fibula, a partial calcaneum, the proximal three fourths of a right ulna, and many bone fragments. Bone breakage and loss occurred during excavation of the well. Because more bones of this animal might still be present at the site, further attempts are being made to recover them (Fig. 3C).

Collectively, the greatest number of mammoth teeth, including tusks, comes from the San Juan de la Vaquería locality near Saltillo, a site that is still

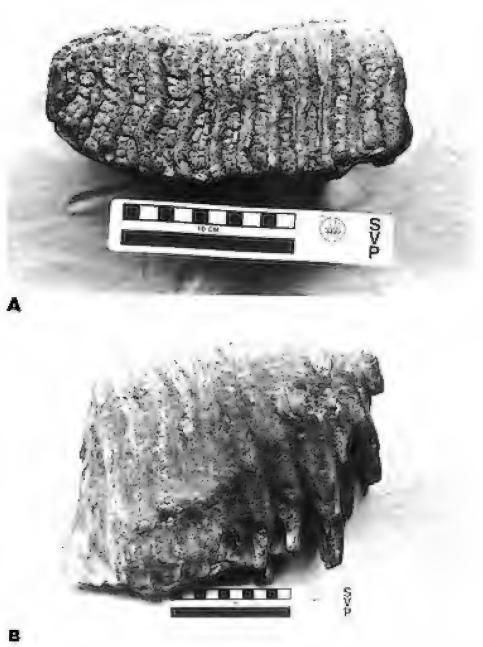

Figure 8 *Mammuthus columbi* (Falconer, 1857), left m3 from Rancho Buena Fe: **A,** occlusal view; **B,** lateral view. Black and white scale bars = 1 cm.

being worked by personnel from the Museo del Desierto. Thus far, large portions of seven tusks have been discovered (only two have been prepared), as well as three complete and 11 incomplete molars. For these molars, the lamellar frequency varies from 6.5 to 8.5 and averages 7.5. The ET varies from 2.0 to 2.8 mm and averages 2.3 mm. To date, only two mammoth bones have been recovered from San Juan de la Vaquería: a scapula and the associated distal part of the humerus. A few complete and incomplete mammoth teeth and tusk portions from Coahuila have been donated to the Museo del Desierto, but without locality data. Every fossil site that is listed in this paper (see Fig. 1) has produced identifiable mammoth specimens, and in some instances, mammoth is the only recognizable fossil.

INFERRED HABITAT. Primarily grasslands and savannas.

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Equus Linnaeus, 1758

Equus Linnaeus, 1758:73.

DISCUSSION. At least two species of *Equus* can thus far be identified from sites in Coahuila. We follow Azzaroli (1998), primarily in recognition of those named from Pleistocene deposits of North America. It is clear from a review of the literature, however, that wide confusion persists in recognition of the valid species within the genus (e.g., Kurtén and Anderson, 1980; Dalquest, 1988; Dalquest and Schultz, 1992; Azzaroli, 1995, 1998). MacFadden (1992) stated that 58 species of *Equus* had been named from Blancan and Pleistocene age deposits in North America, the overwhelming majority of which are of Pleistocene age. Azzaroli (1998) recognized no more than 10 of these as valid. Although most current researchers agree that fewer than 12 species should be accepted, disagreement continues as to which of these are valid. Much of this problem results from inadequate type specimens and original descriptions, as well as from conflicting opinions concerning the diagnostic characters. A number of holotypes are based on inadequate dental material, including isolated teeth (Kurtén and Anderson, 1980; Dalquest and Schultz, 1992).

The problem of identifying valid species of Pleistocene *Equus* will undoubtedly continue well into the future. Intraspecific and interspecific variation has not been sufficiently well documented, despite the report of hundreds of Pleistocene sites in which *Equus* fossils have been recovered, and primarily because the sample sizes at all but a few sites are too small. A complicating factor might have been the result of vegetational and other barriers that formed and were broken during glacial and interglacial intervals. During temporary isolation, populations of *Equus*, as well as other species, might have begun developing distinctive characters, only to have them assimilated into larger populations as barriers disappeared and allowed more open communication for gene interchange.

Several species of *Equus* have been identified in Mexico, particularly in the northern half of the country. A few of these species have been named on the basis of specimens from Mexico: *Equus conversidens* Owen, 1869; *Equus tau* Owen, 1869; *Equus crenidens* Cope, 1884; *Equus mexicanus* Hibbard, 1955; and *Equus parastylidens* Mooser, 1959. *Equus conversidens* and *E. tau*, both representing some of the smallest named Pleistocene species in North America, are said to be mainly distinguishable on the basis of limb bones; dental characters seem ambiguous. *Equus tau* supposedly had long, slender limbs (stilt-legged), whereas the limbs of *E. conversidens* are said to be shorter and much stouter (Kurtén and Anderson, 1980). Hibbard (1955) considered *E. tau* to be a synonym of *E. conversidens*. Azzaroli (1998) as well does not recognize *E. tau* as valid. It is beyond the scope of this paper to include a revision of any *Equus* species, and certainly the amount and nature of the material that has been discovered to date in Coahuila does not warrant this. Identifications of specimens tentatively assigned herein to *Equus* cf. *E. conversidens*,

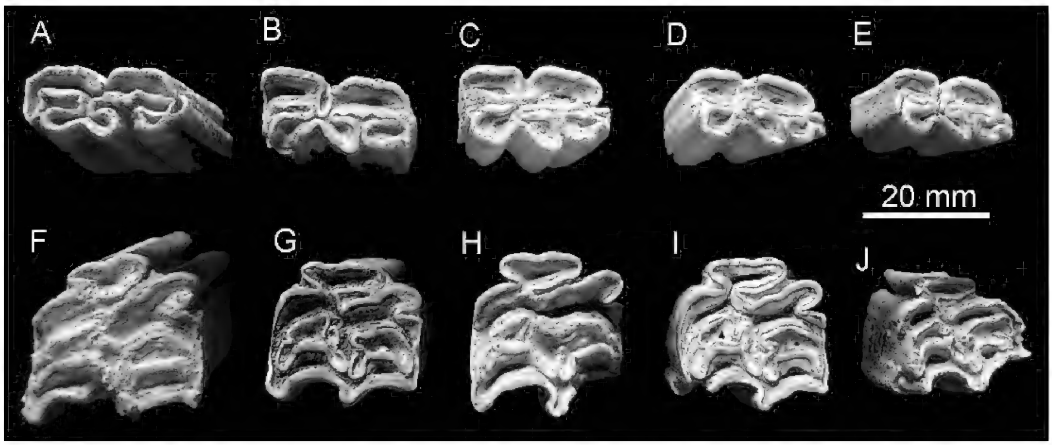

Figure 9 *Equus* cf. *E. conversidens* Owen, 1869; **A–E,** occlusal views of lower cheek teeth; **F–J,** occlusal views of upper cheek teeth from the San Juan de la Vaquería locality: **A,** SEPCP 51/329; **B,** SEPCP 51/327; **C,** SEPCP 51/246; **D,** SEPCP 51/258: **E,** SEPCP 51/254; **F,** SEPCP 51/250; **G,** SEPCP 51/325; **H,** SEPCP 51/231; **I,** SEPCP 51/227; **J,** SEPCP 51/324.

and to *Equus ?excelsus* might require modification when more diagnostic fossils are found.

Equus cf. E. conversidens Owen, 1869

Equus conversidens Owen, 1869:563–565.

REFERRED SPECIMENS. Incisor (SEPCCP 273), upper and lower premolars, and upper and lower molars (SEPCCP 206, 212, 214–216, 220, 226, 227, 231, 233, 236–244, 246, 254, 256–258, 260–262, 264, 265, 267, 324–331) from San Juan de la Vaquería; two thoracic vertebrae (SEPCCP 350), three partial scapulae (SEPCCP 351–353), partial femur (SEPCCP 347), calcaneum, partial astragalus, and ectocuneiform (SEPCCP 354) from Rancho Buena Fe; one upper molar (SEPCCP 372) from the Sabinas region.

DISCUSSION. Descriptions of this species, including its taxonomic history, have been adequately discussed by Hibbard (1955) and Mooser and Dalquest (1975). The physical history of the holotype was reported by Carranza-Castañeda and Miller (1987). Teeth thus far collected from the San Juan de la Vaquería locality indicate the presence of two species of horse at that locality. One is small and the other of medium size. *Equus conversidens* often has been recognized by its small size alone (Dalquest and Schultz, 1992). In addition to its small size, the upper premolars from this site agree well with the descriptions that have been given for the holotype and referred specimens from Mexico (Hibbard, 1955). The only difference noted was the lesser development of enamel plications on the fossettes, a condition that applies to molars as well as to premolars (Fig. 9A).

An illustration of an upper tooth row representing *E. conversidens* (Mooser and Dalquest, 1975:fig. 3) from Aguascalientes, Mexico, shows a matching condition to the teeth from San Juan de la Vaquería. The lower molars here identified as *E. conversidens* cannot be distinguished from the figures and descriptions that can be found in the literature (e.g., Owen, 1869; Dalquest and Schultz, 1992; Azzaroli, 1995, 1998). The present specimens both show a V-shaped linguaflexid, an angular metastylid, and an ectoflexid that extends only to the base of the isthmus (Fig. 9B).

The only equid material found at the Rancho Buena Fe site are postcranial specimens. Although none of these bones is complete, a few are adequate to make meaningful comparisons. Included here are a nearly complete calcaneum, a partial astragalus, and an ectocuneiform of a young individual; two consecutive adult thoracic vertebrae; three incomplete scapulae; and a femur diaphysis. These, and less complete materials, were all compared with equid material housed at the LACM. The most favorable comparisons were made with the horse from San Josecito Cave in Nuevo León, Mexico, which has been identified as *E. conversidens* by Arroyo-Cabrales and Johnson (1995). The specimens from Rancho Buena Fe are either within the size range of the specimens from San Jocecito Cave or are slightly smaller. One exception was a partial vertebra (SEPCCP 355) of a much larger horse (discussed in the "*Equus* sp., *E. ?excelsus*" section). The specimens from Rancho Buena Fe also compare favorably with descriptions of similar elements of an equid that was identified as *E. conversidens* from Dry Cave in Eddy County, New Mexico (Harris and Porter, 1980). Compared with postcranial elements of a female Burchell's zebra in the BYU collections, the specimens from Rancho Buena Fe are slightly smaller.

Equus conversidens has been considered a common small horse during the later Pleistocene from central Mexico to Canada (Mooser and Dalquest, 1975; Kurtén and Anderson, 1980). It has been reported as far south as the Yucatán Peninsula in Mexico (Arroyo-Cabrales and Alvarez, 2003), and reports of *E. conversidens* have been made for areas in the state of Mexico (Córdoba-Barradas et al., 1997; Manrique-Eternod and Villanueva-García, 1997). The present report of this species is the first for the state of Coahuila.

INFERRED HABITAT. Modern horses have long been acknowledged as consummate grazers. With their similar dentitions and skeletal morphology, Pleistocene horses undoubtedly were also grazers. Although both of the extinct Pleistocene horse species from Coahuila basically reflect grassland habitats, the variety of Pleistocene species throughout North America probably indicates some deviation from this standard. Certainly savanna environments would have been included in their habitats.

Equus sp., *E.* ?*excelsus* Leidy, 1858

Equus excelsus Leidy, 1858b:26.

REFERRED SPECIMENS. Incisors (SEPCCP 270, 332) and upper and lower premolars and molars (SEPCCP 207–209, 211, 217, 219, 223, 224, 228, 229, 232, 235, 237, 238, 245, 248, 255, 266, 268, 269, 333–336) from San Juan de la Vaquería; partial thoracic vertebra (SEPCCP 355) from Rancho Buena Fe; two lower molars (SEPCCP 339) from El Durazno; two upper molars (SEPCCP 373) from Sabinas region.

DISCUSSION. Although Azzaroli (1998) described *E. excelsus* as being "a species of rather large size," Mooser and Dalquest (1975) stated that medium size is one of the diagnostic features of this horse. Dalquest and Schultz (1992) also referred to this species as a medium-size horse. Of course large, medium, and small are relative terms, useful only in a general way. As with most other *Equus* species, there is a complex nomenclatural history involved with *E. excelsus*, many possible synonymies exist, and Savage (1951) considered it to be a *nomen vanum*. A thorough revision of the species is needed.

Mooser and Dalquest (1975) gave what they listed as defining characters for the dentition of *E. excelsus* from the Cedazo Local Fauna of Aguascalientes. For upper cheek teeth, the enamel pattern was said to be simple, the styles strong and prominent, and the protocone relatively short and broad, usually with a lingual groove. The upper premolars and molars from San Juan de la Vaquería fit this description well, with the exception that the protocones are not all "relatively short." Of course, this feature can vary somewhat with wear. In the lower dentition it was stated by Mooser and Dalquest (1975) that the protoconid–hypoconid valley (= ectoflexid) does not pass between the metaconid–metastylid complex (i.e., into the isthmus), except in some worn molars; that the metaconid is rounded, usually larger than the pinched and angular metastylid; and that the metaconid–metastylid valley (= linguaflexid) presents a broadly V- to U-shaped pattern. The lower premolars and molars from San Juan de la Vaquería fit this description. Also, their sizes compare favorably with those from the Cedazo Local Fauna. Nevertheless, with so much confusion in the literature concerning medium- and large-size Pleistocene horses of North America, especially regarding isolated teeth, the present material is only questionably assigned to *E. excelsus*. The partial vertebra from Rancho Buena Fe might also be assignable to this species.

Equus crenidens was based on a maxilla with three premolars from the Valley of Tequixquiac in the state of Mexico, but there is some doubt as to the validity of the species (Azzaroli, 1998). Hibbard (1955) designated a fragmentary maxilla with P2 and P3 from the same valley as the neotype for this species in lieu of the lost holotype. Descriptions of the holotype and neotype, as well as of many referred specimens of *E. crenidens*, were also compared with the upper premolars of the larger horse from San Juan de la Vaquería. Dimensions listed by Hibbard (1955) for the holotype and neotype are significantly larger than for the same ones of the current two premolars. Additional characters given were short protocones, complex enamel patterns of the fossettes, and a well-developed pli caballin. The characters for the premolars in the present sample include elongate protocones, simple enamel patterns in the prefossettes and postfossettes, and usually no more than a very small pli caballin.

INFERRED HABITAT. Grasslands and savannas.

Order Artiodactyla Owen, 1848

Family Camelidae Gray, 1821

DISCUSSION. Information on the origin of camels and most of their history comes from deposits of Eocene through Pleistocene age in North America. Some of the geochronologically youngest records of camels on this continent are from archeological sites at about the Pleistocene–Holocene boundary (Frison et al., 1978). Frison et al. (1978) stated that *Camelops* Leidy, 1854, was present at two kill sites near Casper, Wyoming, where the animals were apparently butchered. Frison (2000) in a re-evaluation of this site, stated that the age of these presumably butchered camels is older by more than 1,000 years than was earlier estimated. The youngest possible age for these camel fossils was given by Frison as 11,190 ± 50 yr BP.

Camels might have arrived in South America as early as the early Pliocene, when the Panamanian Isthmus was first formed (Carranza-Castañeda and Miller, 2004). *Hemiauchenia* Cope, 1893, a North America–originating camel, has been reported in South America from early Pleistocene deposits (Webb, 1974; Marshall, 1985). Camels live now in South America as llamas and their kin.

According to Kurtén and Anderson (1980), six genera of camels inhabited North America during the Pleistocene. However, two of these, *Blancocamelus* Dalquest, 1975, and *Megatylopus* Matthew and Cook, 1909 (the latter being poorly known), apparently did not survive the Blancan NALMA. The remaining four genera—*Titanotylopus* Cope, 1893; *Camelops*; *Hemiauchenia*; and *Palaeolama* Gervais, 1867—are reasonably well represented in the Pleistocene of North America. This is especially true of *Camelops* and *Hemiauchenia*, which are both widespread in deposits of the western part of the continent. Both of these genera have been reported from many sites from central Mexico through Canada, with *Camelops* also occurring in Alaska. On the basis of the size of the specimens, none of the camelid fossils thus far discovered in Coahuila belong to the giant form *Titanotylopus*. However, with the use of size as a criterion, two smaller genera can now be recognized from this state for the first time, as follows.

Camelops cf. *C. hesternus* (Leidy, 1873)

Auchenia hesterna Leidy, 1873:259–260.

REFERRED SPECIMENS. Right and left m3 (SEPCCP 318), metatarsus (SEPCCP 319), and vertebral centrum (SEPCCP 298) from El Durazno; P4–M1 (SEPCCP 363), two lower incisors (SEPCCP 359), m1 (SEPCCP 360), and molar fragments (SEPCCP 361) from San Juan de la Vaquería; two lumbar vertebrae and partial sacrum (SEPCCP 356) from Rancho Buena Fe; dentary fragment with partial m2–3 (SEPCCP 375) and partial thoracic vertebra (SEPCCP 376) from the Sabinas region.

DISCUSSION. Although the number of named species and confusion of nomenclatural history of *Camelops* does not closely approach those for *Equus*, there is still no general agreement about which species of *Camelops* should be recognized. Dalquest and Schultz (1992) mentioned some problems that exist in *Camelops* taxonomy. According to them, dental characters are of little value in distinguishing species. Kurtén and Anderson (1980) listed six valid North American species. These are *Camelops kansasensis* Leidy, 1854; *Camelops traviswhitei* Mooser and Dalquest, 1975; *Camelops sulcatus* (Cope, 1893); *Camelops huerfanensis* (Cragin, 1892); *Camelops minidokae* Hay, 1927; and *C. hesternus*. The first species listed above is the genotypic species; however, its validity has been questioned, and Webb (1965) listed it as a *nomen dubium*. He said that although specimens have been referred to *C. kansasensis* from time to time, he knew of no adequate basis for confirming or rejecting such determinations. The genus *Camelops* is so well ingrained in the literature, that it certainly should be maintained. Kurtén and Anderson (1980) felt that *C. huerfanensis* probably is a synonym of the earlier named *C. hesternus*.

A complete right metatarsus and a vertebral centrum of an adult camel were discovered at the El Durazno locality, where an earlier discovery was made of two m3s. The length of this metatarsus is within the range of variation for *C. hesternus* metatarsi from Rancho La Brea in California (Webb, 1965). The length of the metatarsus from El Durazno is 36.7 cm, and the mean for those measured by Webb from Rancho La Brea is 37.6 cm, with the shortest being 35.7 cm. Transverse and anteroposterior measurements of the metatarsus from El Durazno are slightly less than seven metatarsi from Rancho La Brea that were measured by Webb. This does not seem to be a significant difference. The measurements of the two m3s from El Durazno (Fig. 10A), which undoubtedly are from the same individual (and probably a different individual than the one represented by the metatarsus; Fig. 10B), are within the size range for this lower molar as given by Webb (1965). Measurements for anteroposterior and transverse diameters, respectively, of the two teeth from El Durazno are: right m3, 58.0 by 19.2 mm, and left m3, 57.7 by 19.3 mm.

Two associated lumbar vertebrae and a sacrum of a large camel, probably belonging to the same individual, were recovered at the Rancho Buena Fe locality. One of the lumbars, the seventh, articulates correctly with the sacrum. This material was compared with specimens identified as *C. hesternus* at the LACM and falls within the range of variation of those specimens. Webb (1965), in presenting tables of measurements, listed lumbars as "early," "middle," and "late." A first or second lumbar from Rancho Buena Fe, as well as the seventh, were both in accord with measurements given by Webb (1965). Although the posterior portion of the sacrum from Rancho Buena Fe is missing, its anterior dimensions fall within parameters that were given by Webb for *C. hesternus* from Rancho La Brea.

A third site in Coahuila yielding a large camel is San Juan de la Vaquería, and this site also contained fossils of a small camel species that is discussed below. Both camelids are represented by lower dentitions. Teeth of the larger camel include i2 and i3, two m1s (or possibly an m1 and an m2), and two m3s (one of the m3s is broken, but its size appears to be the same as the one with measurements listed below). These teeth might all be from a single young adult individual. Mea-

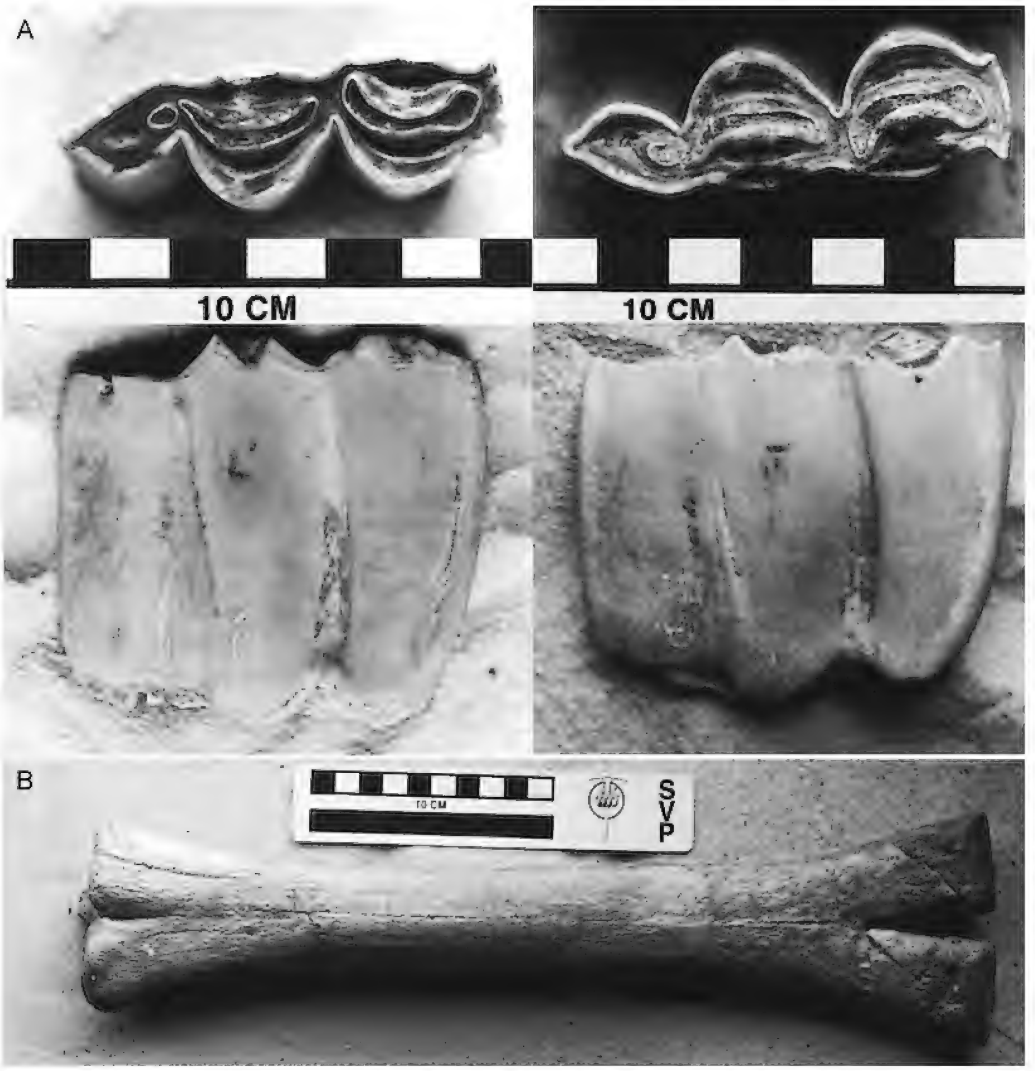

Figure 10 *Camelops* cf. *C. hesternus* (Leidy, 1873); **A,** right and left m3 (occlusal and lingual views); **B,** metatarsus from El Durazno. Black and white scale bars = 1 cm.

surements of the m3 made on the occlusal surface (the base and widest part of this tooth is missing) are: greatest anteroposterior length, 58.0 mm; transverse width, 20.2 mm. Although the length of this tooth is significantly greater than four measurements that were given by Webb for this parameter, it is very close to a young adult m3 of a specimen from Sonora, Mexico, that was referred to *C. hesternus* by Lucas and Ortega-Guerrero (1998). The m1 (or m2) measures 39.1 mm anteroposteriorly and 18.2 mm transversely.

Another specimen of a mature large adult camel is from the same locality. It is a small maxillary fragment containing the P4 and M1. Both of these teeth are worn but complete, and they represent a different animal than the young adult described above. The P4 measures 25.7 mm anteroposteriorly and 23.1 mm transversely, and the M1 measures 29.3 mm anteroposteriorly and 31.2 mm transversely. These measurements also are within the range that was given for corresponding teeth of *C. hesternus* by Webb (1965). However, the dentary fragment from Sabinas (SEPCCP 375), containing a broken m2 and m3, represents a mature animal. It does seem to be *Camelops*, but if it is *C. hesternus*, then it is a very small individual. The only measurement that can be made with confidence is the m3 anteroposterior length of 37.5 mm.

Mooser and Dalquest (1975) named *C. travis-whitei*, from the Cedazo Local Fauna. They

diagnosed it as a camel the size of, or larger than, *C. hesternus*. It reportedly has lakes in the molars that possess sharp V-shaped, rather than broadly rounded, figures. If this truly represents a distinct species, it is somewhat larger than the *Camelops* from Coahuila, which has molars with broadly rounded lakes. Both *C. sulcatus* and *C. minidokae* are significantly smaller than *C. hesternus*. With the questionable status of both *C. huerfanensis* and *C. kansasensis*, it seems best to refer the large camelid fossils from Coahuila to *C. hesternus*, which is, in fact, the best recognized species in western North America.

INFERRED HABITAT. Hibbard and Taylor (1960) indicated that *Camelops* inhabited open shrub and grassland areas. Considering the associated animals that have been found at numerous localities, this seems to be a preferred habitat. The occurrence of this species at the three known sites in Coahuila, with the associated faunas at each, further substantiates this interpretation.

Hemiauchenia macrocephala (Cope, 1893)

Hemiauchenia cf. *H. macrocephala*

Holomeniscus macrocephalus Cope, 1893:85.

REFERRED SPECIMENS. Lower incisor (SEPCCP 357), left m2–3 (SEPCCP 322), right m2 (SEPCCP 272) from San Juan de la Vaquería.

DISCUSSION. A small camel is recognized in the San Juan de la Vaquería Local Fauna on the basis of associated m2 and m3 with stages of wear that suggest they are from a single individual. The bases of all three teeth from this locality are missing. The right m2 (SEPCCP 272) measures 27.7 mm anteroposteriorly and 20.0 mm in greatest transverse width. The left m2 measures 28.3 mm anteroposteriorly and 15.1 mm in greatest transverse width, and the measurements of the m3 at similar points are 29.5 and 14.1 mm. A partial lower incisor might also belong to this same individual. The anterior stylid ("llama buttress") on both m2 and m3 are moderately well developed, more so on the m2 than on the m3. Although Webb (1974) stated in the diagnosis of *Hemiauchenia* that llama buttresses are weak, Breyer (1977), referring to specimens from Nebraska, said that this feature was moderately well developed on some lower molars of that genus. Both teeth from San Juan de la Vaquería show marked hypsodonty.

Dalquest and Schultz (1992) postulated that most of the numerous species names that have been proposed for *Hemiauchenia* appeared to be invalid. Breyer (1977), in his study of an exceptionally large sample of *Hemiauchenia* specimens from the Broadwater Formation in Nebraska, said that most characters on which the various named species have been based represent ontogenetic stages, or aspects of individual variation. He recognized only three valid species: *Hemiauchenia vera* (Matthew, 1909); *H. macrocephala*; and *Hemiauchenia blancoensis* (Meade, 1945). *Hemiauchenia seymourensis* (Hibbard and Dalquest, 1962) was considered to be a synonym of the *H. blancoensis*. Only one other genus of relatively small camel, *Palaeolama* Gervais, 1867, has been positively identified from the Pleistocene of North America. It is apparently represented by a single species on this continent, *Palaeolama mirifica* (Simpson, 1929), but other species are known in South America (Webb, 1974). As stated by Webb in 1974, *Hemiauchenia* can be distinguished from *Palaeolama* on the basis of its lower dentition, having greater hypsodonty and a better developed llama buttress. The p4 in *Palaeolama* was also said by Webb to be more complex than in *Hemiauchenia*, with multiple fossettids. Although no p4 has yet been found of any camel from San Juan de la Vaquería, all of the above characters serve to identify the small camel at San Juan de la Vaquería as *Hemiauchenia* rather than *Palaeolama*. Because *H. vera* has been identified from Hemphillian age deposits, and *H. blancoensis* has only been reported from the Blancan (Breyer, 1977), just a single Pleistocene species, *H. macrocephala*, appears valid for North America. Also Dalquest and Schultz, (1992) doubted whether *H. blancoensis* could be distinguished from *H. macrocephala*, which has priority.

Most fossils of *Hemiauchenia* have been from the western United States. The genus has been identified as far south as the Loltún Cave in the Yucatán Peninsula of Mexico (Arroyo-Cabrales and Alvarez, 2003, in which no species identification was made), and from central to northern Mexico. Our present record is the first for the genus from Coahuila.

INFERRED HABITAT. Grasslands and savannas.

Family Cervidae Gray, 1821

Odocoileus virginianus (Zimmermann, 1780)

Odocoileus ?virginianus

Dama virginiana Zimmermann, 1780:129.

REFERRED SPECIMENS. Partial left antler (SEPCCP 349) and the distal end of a left humerus (SEPCCP 348), both from Rancho Buena Fe.

DISCUSSION. The white-tailed deer, *O. virginianus*, and the black-tailed or mule deer, *Odocoileus hemionus* (Rafinesque, 1817), have been identified as fossils at numerous Pleistocene sites throughout the United States and Canada. Fossils of *Odocoileus* (Zimmerman, 1780), however, reportedly are rare in Mexico. Antlers, or parts thereof, are the most recognizable part of the skeleton to be preserved. Because antlers are

the most diagnostic element for species identification (as with horn cores for antilocaprids), this specimen (SEPCCP 349) is important. The distal end of the humerus is not diagnostic, other than to family, but because it is from the same locality, we consider it to be conspecific with the antler.

Both major tines of the antler from Rancho Buena Fe are broken about halfway from the point of branching to their tips. The brow tine is large and complete, forming about 7 cm above the base. From the burr, where the antler was shed in life, to the end of the highest tine, the greatest height is approximately 13 cm. Rugosity near the base of the antler is minimal. Although antlers can generally be used to distinguish between adult *O. virginianus* and *O. hemionus*, the distinction becomes much less clear with young individuals. On the basis of antler development, the present specimen probably represents an animal that was no more than two years of age. At this stage the white-tailed and black-tailed deer have antler morphologies that do not markedly differ when the full range of variation is considered. Comparisons between the fossil and a number of young white-tailed and black-tailed deer in the collections at BYU were made, which showed that the deer from San Juan de la Vaquería fit a pattern most like that of *O. virginianus*; however, the identification cannot be conclusive. The white-tailed deer is generally, but not always, the smaller of the two species, a factor that was also considered in identifying the Mexican specimen. Both species today inhabit the State of Coahuila, but *O. virginianus* is the more common and widespread of the two.

INFERRED HABITAT. Forests and woodlands, including riparian environments.

Family Antilocapridae Gray, 1866

Capromeryx cf. *C. mexicana* Furlong, 1925

Capromeryx mexicana Furlong, 1925:145–152.

REFERRED SPECIMENS. A right m3 (SEPCCP 367) from San Juan de la Vaquería.

DISCUSSION. Unfortunately, the genus *Capromeryx* Matthew, 1902, like so many other genera and species of Pleistocene mammals, has a complex nomenclatural history. This was addressed in large measure by Morgan and Morgan (1995) when they described a new species from the state of Washington, *Capromeryx tauntonensis*. Dalquest and Schultz (1992) indicated that workers have described more species of antilocaprids than the fossil materials justify. Kurtén and Anderson (1980) offered the opinion that Pleistocene antilocaprids are in need of revision.

Currently, five genera of Pleistocene pronghorns are recognized in North America: *Tetrameryx* Lull, 1921; *Stockoceros* Frick, 1937; *Hayoceros* Frick, 1937; *Capromeryx*; and *Antilocapra* Ord, 1818. The first three of these genera show close relationships, and they might or might not represent three distinct genera (see Simpson, 1945:157). *Capromeryx* is the genus that includes by far the smallest species. However, the Blancan species of *Capromeryx* from Washington that was described by Morgan and Morgan (1995) approaches the living *Antilocapra americana* (Ord, 1815) in size. Of the Pleistocene species of *Capromeryx*, Morgan and Morgan (1995) and Kurtén and Anderson (1980), considered only four valid: *Capromeryx furcifer* Matthew, 1902, which is the genotypic species; *Capromeryx minor* Taylor, 1911; *C. mexicana*; and *Capromeryx arizonensis* Skinner, 1942.

Because fossil antilocaprids have been named on the basis of horn cores and only an m3 is known from a single site in Coahuila, at San Juan de la Vaquería, the present specimen can only be tentatively referred to a species. The very small size of the m3 alone distinguishes it as *Capromeryx*. Its anteroposterior length measures 12.5 mm and its transverse width is 4.7 mm. A young individual is indicated by the height of the tooth (37.1 mm) and by the minimal wear across the occlusal surface.

Capromeryx mexicana was named by Furlong (1925) for a tiny antilocaprid from near Tequixquiac in central Mexico. Mooser and Dalquest (1975) referred a similar-sized antilocaprid from the Cedazo Local Fauna of Aguascalientes to this species, saying that this identification was based on probability. The same holds true for the present specimen. Further work, however, is needed to clearly determine the validity of this species when critically compared with an adequate sample size of *C. minor*. *Capromeryx furcifer* appears to be larger than either *C. minor* or *C. mexicana*.

Thus far, *C. mexicana* has been recognized only in presumably later Pleistocene deposits in Mexico. *Capromeryx* sp. has been reported from a few other sites in central Mexico (Manrique-Eternod and Villanueva-García, 1997), as well as from the northwestern state of Chihuahua (Messing, 1986). Although the antilocaprid *Stockoceros conklingi* Stock, 1930, is common in the San Jocecito Cave Local Fauna (Arroyo-Cabrales and Johnson, 1995), *Capromeryx* is not. This might result from the more rugged terrain and woodland cover in the vicinity of San Josecito Cave, which was probably more heavily vegetated in the Pleistocene.

INFERRED HABITAT. Primarily grasslands and open areas.

AGE AND ENVIRONMENTAL INTERPRETATIONS

AGE

Although the ages of the fossil-bearing sediments reported in this paper vary, certainly they all fall within the Pleistocene Epoch, and in our opinion,

as a composite assemblage, they best fit a Rancholabrean NALMA. This is based on the two available radiocarbon dates and the compositions of the assemblages at the various sites. All of the fossil sites reported here contain teeth of *M. columbi*, and this species is generally regarded as being restricted to the Rancholabrean NALMA (Agenbroad, 2003).

Wood found in association with the fossils at Rancho Buena Fe has been radiocarbon dated at 11,740 ± 50 BP. It was processed at the Radiocarbon Laboratory at UCR. A wood sample collected at the El Durazno site associated with fossil vertebrates was dated at the laboratory of Beta Analytic, Inc., in Miami, Florida. Results of the analysis of this sample yielded an age of 41,110 BP. Samples of bone from the San Juan de la Vaquería site were processed at this lab, but a lack of collagen in these specimens prevented an age determination. Nevertheless, the presence of *M. columbi*, and probably of *Equus* cf. *E. conversidens*, as well as *Capromeryx* cf. *C. mexicana*, imply a late Pleistocene age. Ages have previously been determined for bones and plant material from packrat middens in central Coahuila. Only the plant material was dated as being as old as the latest Pleistocene. All vertebrate material was Holocene in age (Van Devender and Burgess, 1985; Van Devender and Bradley, 1990).

ENVIRONMENTAL INTERPRETATIONS

Because the time represented by the various fossiliferous sites is late Pleistocene, geologic and geographic conditions must have been nearly the same as they are at present, but the climate was undoubtedly very different. The state of Coahuila covers a large area with dramatic differences in elevation, so conditions probably varied considerably within the state. Several studies have concentrated on climatic changes, especially in the central region of Coahuila. Van Devender and Burgess (1985:346), working on packrat middens, stated that, "an equable late Wisconsin climate marked by mild winters with increased precipitation and by cool summers with reduced summer monsoons is proposed."

Presenting a differing view for this same region, Meyer (1973:982) said that, "comparisons of modern pollen spectra from the [Cuatro Ciénegas] basin floor with the fossil records indicate that vegetation ecologically equivalent, if not identical, to that now present has occupied the floor of the basin since mid-Wisconsin time."

On the basis of the late Pleistocene fossils discussed in this paper, which represent at least part of late Wisconsin time, it seems that the amount of rainfall must have been greater than it is at present. Herds of horses, camels, mammoths, and antilocaprids, as well as other species favoring grasslands, indicate a grassland habitat that does not now exist in the area. These grasslands were no doubt interrupted by woodland areas as well, on the basis of the presence of deer and mastodon. The fact that the mastodon at Progreso was recovered from a locality at an elevation of 300 m suggests that woodlands, or at least wooded riparian habitats, existed at this low elevation during late Pleistocene time in Coahuila.

CONCLUSIONS

1. Prior research on Pleistocene vertebrate paleontology, as well as geology, in the state of Coahuila, Mexico, has been essentially lacking.
2. This paper constitutes the first report of a fossil vertebrate fauna from Coahuila.
3. The twelve Pleistocene mammalian species listed herein have not been previously reported from Coahuila. These are *Sylvilagus ?leonensis* (cottontail), cf. *Lepus* sp. (jack rabbit), *Pappogeomys* cf. *P. castanops* (gopher), *Canis* cf. *C. latrans* (coyote), *Mammut americanum* (American mastodon), *M. columbi* (Columbian mammoth), *Equus* cf. *E. conversidens* (horse), *Equus* sp., *E. ?excelsus* (horse), *Camelops* cf. *C. hesternus* (camel), *Hemiauchenia* cf. *H. macrocephala* (llama), *Odocoileus ?virginianus* (deer), and *Capromeryx* cf. *C. mexicana* (pronghorn).
4. Both radiocarbon dates, and some of the age-restricted species (e.g., *M. columbi*, *Equus* cf. *E. conversidens*, and *Capromeryx* cf. *C. mexicana*), indicate a late Pleistocene age for the aggregate fauna.
5. The presence of grazing and browsing animals suggests that grasslands as well as woodlands existed in the State of Coahuila during late Pleistocene time.
6. Notably absent from the assemblage are ground sloths, large carnivorans (such as wolves, bears and cats), and bison. Amphibians, reptiles, birds, and small mammals are absent or underrepresented, but screen washing could increase our knowledge of such members of the late Pleistocene fauna of Coahuila.

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Late Pleistocene distribution of *Bison* (Mammalia; Artiodactyla) in the Mojave Desert of Southern California and Nevada

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ABSTRACT. A review of fossils of extinct *Bison* from the Mojave Desert of California and Nevada demonstrates that the genus is even rarer in the region than was previously thought. The presence of fossils resembling *Bison antiquus* is confirmed only from the Las Vegas Valley, China Lake, Lake Manix (high in the section), and Dove Spring Wash. Additionally, a magnum of a very large *Bison* is present from a locality at Twentynine Palms. Other published records of *Bison* from the Mojave are problematic. Fossils assigned to *Bison* cf. *B. antiquus* from older (~290 Ka) sediments at Lake Manix are actually *Camelops*. A reported occurrence of *Bison* from the Pinto Basin is also *Camelops*. Fossils previously assigned to *Bison* sp. from the Piute Valley are an indeterminate large bovid and a large *Equus*. *Bison* is presently considered to have arrived in North America south of the ice between 210 ± 60 Ka and approximately160 Ka. Radiometric dates for confirmed occurrences of the genus *Bison* in the Mojave Desert range from less than 144 to 15 Ka and possibly 11 Ka in the Las Vegas Valley to between approximately 35 and 19 Ka at Lake Manix, about 19 Ka at China Lake, and approximately 16 Ka at Dove Spring Wash. The observed date range accords well with the age of coastal and inland Southern California records of extinct *Bison* (e.g., Rancho La Brea, Diamond Valley Lake, etc.), which are also relatively young. Fossils of *Bison* in the Mojave Desert have no older dates. The observed distributions and ages of *Bison* in the Mojave Desert and the southwest suggest that the genus might have had a more restricted temporal range than previously thought. This has important implications for biostratigraphy, for regional paleoecological reconstructions, and for correct interpretations of megafaunal representation and diversity at the end of the Pleistocene.

INTRODUCTION

In 1990, a late Pleistocene large mammal fauna was recovered from the northwestern Mojave Desert from a sequence of unnamed Quaternary stream and pond deposits in Dove Spring Wash, Red Rock Canyon State Park, Kern County, California (Whistler et al., 1991; Scott et al., 2001). This fauna included a partial skeleton of an extinct bison, *Bison antiquus* Leidy, 1852 (Whistler et al., 1991; Scott et al., 2001). The recovery of this partial skeleton prompted a review of previous records of fossils of the genus *Bison* Hamilton-Smith, 1827, from the Mojave Desert so to better assess the significance of the new find.

This review revealed that no detailed specimen descriptions were available for any of the published records of *Bison* from the Mojave Desert and that most records were simply reports in faunal lists. It therefore became necessary to examine directly the fossils on which these published records were based to evaluate the accuracy of these reports. This examination resulted in the refinement of some published identifications, particularly with regard to species assignments, and in the referral of some purported specimens of *Bison* to other taxa altogether. These emendments provide data critical for correctly interpreting species diversity and paleoenvironmental settings in the late Pleistocene deposits of the Mojave Desert, as well as for better clarifying the Pleistocene biostratigraphy of the region.

Jefferson (1991b) listed approximately 50 late Pleistocene localities yielding remains of large mammals from the Mojave Desert of Southern California; more than 32 additional localities are recorded from southern Nevada (Harris, 1985; Heaton, 1990). Some of these localities are single sites, others are multiple sites in a limited geographic area, and some are relatively broad geographic regions containing numerous discrete fossil loci within a single formation. A modified list of these localities, with some clusters of multiple sites subsumed under single locality names where appropriate, is presented in Table 1.

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Table 1 List of vertebrate faunas of reported late Pleistocene age from the Mojave Desert, with reported large ungulates. Includes published data from Harris (1985), Heaton (1990), Jefferson (1991a, 1991b), Weinstock et al. (2005), and Scott et al. (2006). Presence of a genus is denoted by "X"; multiple species of a genus are denoted by the appropriate numeral. See text for discussion. **ABBREVIATIONS: M** = *Mammuthus*; **E** = *Equus*; **C** = *Camelops*; **H** = *Hemiauchenia*; **A** = *Antilocapra*; **Od** = *Odocoileus*; **Ov** = *Ovis*; **B** = *Bison*; **cf.** = compares favorably; **?** = possible occurrence; **Irv** = Irvingtonian; **RLB** = Rancholabrean.

Locality	Sites	Date	M	E	C	H	A	Od	Ov	B
Clark County										
Boulder City	1	late Pleistocene							X	
Centennial Parkway	1	RLB	cf.	2	X		?			
Corn Creek Springs (PR3)	1	~14,300		X	X					
El Dorado Wash	1	?RLB	X							
Elephant Hill	1	?RLB	X							
Glendale	1	< >33,000	X	X	X			X	X	
Gypsum Cave	1	≥33,9Ka to ~13Ka		2	X	X		X	X	
Las Vegas Valley	50+	<144Ka to ~10.5Ka	X	2	X	X	X	X		X
Moapa	1	RLB	X	X						
Pintwater Cave	1	≤~31,899							X	
Potosi Midden #2	1	≤~16,370						X		
Richardson's Ranch	1	RLB			X					
Searchlight	1	?RLB		X	X					
Inyo County										
Lake Tecopa	2+	Blancan–RLB	X	2-3	X	2		X		
Kern County										
China Lake	4	~18.6Ka to ~11.8Ka	X	2	X	X		X		X
Dove Spring Wash	5	~19.2Ka to ~16.9Ka	X	X	X			X		X
Goler Gulch	1	RLB		X						
Rodgers Dry Lake	11+	Part Holocene	?	X	?	cf.				
Riverside County										
Pinto Basin, Joshua Tree	4+	?RLB	X	2	X	X		X	X	
San Bernardino County										
Antelope Cave	1	11,080 ± 160		X	X	X	X		X	
Awl Site	1	?RLB	X							
Bedford Road	1	RLB		X						
Bitter Springs Playa	1	RLB	X	2	X	X		X		
Black Butte, Newberry	2?	?RLB	X		X					
Broadwell Lake	7	RLB					?			
Calico Road	11	RLB		X	X					
Daggett	13	≤~12.21Ka	X	X	X	X				
Danby Lake	1	RLB		X						
Ft. Irwin Art. Range #10	1	Irv or RLB		X						
Kingston Wash	1	RLB	X	X						
Kokoweef Cave	1	9,850 ± 160		X	X		X	X	X	
Kramer	7	RLB		X		X	X			
Lake Manix	~180	≤350Ka to >19Ka	X	2–3	X	X	X		X	X
Ludlow Cave	1	RLB				X				
Mescal Cave	2	RLB		X						
Mitchell Cavern	2+	?Part Holocene		X	X				X	
Newberry Cave	1	Part Holocene		X					X	
Old Spring, Needles	1	RLB		X	X					
Piute Valley	6	RLB		X	X					?
Rabbit Springs	1	RLB		X	?					
Saltmarsh, Danby Lake	7	RLB		X	X					
Sands Lacustrine	8	RLB	X	2	X					
Schuiling Cave	2	Part Holocene		2	?	X			X	
Twentynine Palms	6+	?RLB	X	X	X	X		X	X	X
Valley Wells	17	Blancan–RLB	X	2	X	X	?			
Victorville	40+	Irv; RLB?	X	X	X	X				
Yermo	3+	≤~12.8Ka		2	X	X			X	

Commonly represented large mammal taxa include, in decreasing order of representation, *Equus* Linnaeus, 1758 (36 localities); *Camelops* Leidy, 1854 (≥26 localities); *Mammuthus* Brookes, 1828 (≥18 localities); *Hemiauchenia* Gervais and Ameghino, 1880 (≥13 localities); *Ovis* Linnaeus, 1758 (12 localities); *Odocoileus* Rafinesque, 1832 (10 localities); and *Bison* (5 localities).

The late Pleistocene age of many of these sites can be demonstrated on the basis of radiometric dates or inferred on the basis of the presence of late Pleistocene taxa such as *Mammuthus columbi* (Falconer, 1857) and extinct *Bison* spp. (Table 1). Following the taxonomy proposed by Maglio (1973) and advocated by Agenbroad (1984) and Graham (1986), among others, *M. columbi* is here considered a late Pleistocene species. The geologic age of this species is estimated to have ranged from 130,000 years ago (130 Ka) to approximately 10 Ka (Agenbroad, 1984).

METHODS AND MATERIALS

ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York USA
DMNS	Denver Museum of Nature and Science, Denver, Colorado USA
GCPM	George C. Page Museum, Los Angeles, California USA
IMNH	Idaho Museum of Natural History, Pocatello, Idaho USA
KU	Natural History Museum, University of Kansas, Lawrence, Kansas USA
LACM	Natural History Museum of Los Angeles County, Los Angeles, California USA
MM	Maturango Museum, Ridgecrest, California USA
MNI	Minimum number of individuals
NALMA	North American Land Mammal Age
NISP	Number of identified specimens
SBCM	San Bernardino County Museum, Redlands, California USA
SDSNH	San Diego Natural History Museum, San Diego, California USA
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
UCR	Department of Geological Sciences, University of California, Riverside, California, collections and records now maintained at the Museum of Paleontology, University of California, Berkeley, California USA

Fossils of extinct *Bison* from the Mojave Desert were examined in the following collections: the Division of Geological Sciences, SBCM; the Department of Geological Sciences, UCR; the Section of Vertebrate Paleontology, LACM; the MM; and the Department of Paleontology, SDSNH. Comparative specimens of *Bison*, *Bootherium*, *Camelops*, and *Equus* in the collections of SBCM, LACM, DMNS, GCPM, IMNH, and KU were employed to assess the identifications of fossils of *Bison* from the Mojave Desert. Fossils of *Bison* from the Tule Springs site in the collections of AMNH were not available for examination during this study because of an ongoing asbestos abatement program in those collections.

During the course of this study, fossils housed at UCR were transferred *in toto* to the collections of UCMP. Specimen numbers have been amended to reflect the catalogues of UCMP, in every case by adding the numeral "3" at the front of the original UCR specimen number (e.g., UCR 10513 becomes UCMP 310513).

The primary focus of this study was to locate and describe specimens of *Bison* from the Mojave Desert that have been previously reported in faunal lists but not otherwise diagnosed in published accounts. In some cases, particularly China Lake and the Las Vegas Valley, fossils were too numerous to permit a full systematic description of each element recovered. In the case of China Lake, voucher specimens are briefly assessed herein. In the case of fossils from Tule Springs and the Las Vegas Valley, these were briefly described and figured elsewhere (Simpson, 1933; Mawby, 1967; McDonald, 1981). The published diagnoses for these fossils are correct, so further elaboration of them was not considered necessary, and they are not discussed in any great detail. Measurements were acquired from voucher specimens from this sample, however.

Measurements were taken following the procedures outlined by Von den Driesch (1976). Data were acquired with the use of Mitutoyo Digimatic calipers connected by a Mitutoyo MRS100 caliper interface cable to a Hitachi VisionBook Plus 5000 computer running the CalExcel caliper interface program (32-bit version for Windows 95/NT). Graphic plots were generated with SigmaPlot 8.0.

DEFINING THE RANCHOLABREAN NORTH AMERICAN LAND MAMMAL AGE

The Rancholabrean NALMA, named for the mammal assemblage from the Rancho La Brea asphalt deposits in Los Angeles, California (Savage, 1951), is characterized by the presence of the Eurasian immigrant genus *Bison* south of 55°N latitude (Bell et al., 2004). The timing of the arrival of *Bison* in the coterminous United States has not been determined with any certainty, and so the beginning of the Rancholabrean is not reliably established. Recent studies suggest a beginning date younger than about 300 Ka, but estimates vary (Lundelius et al., 1987; Sanders, 2002; Bell et al., 2004; Scott, 2004).

Repenning (1987) proposed defining the Rancholabrean NALMA using the immigration of *Lagurus* Gloger, 1841, and various species of *Microtus* Schrank, 1798, and placed the beginning of the Rancholabrean at 450 ± 25 Ka. The Rancholabrean NALMA was subdivided into two events, Rancholabrean I and Rancholabrean II, with the latter beginning 150 ± 25 Ka and characterized by the presence of *Dicrostonyx* Gloger, 1841, and *Lemmus* Link, 1795, as well as several living species of *Microtus*. Rancholabrean I faunas were explicitly defined as predating the arrival of *Bison* in the United States (Repenning, 1987). Subsequent to this study, Repenning et al. (1990) reinterpreted this chronology because of the formal adoption of *Bison* as the defining taxon for the Rancholabrean by Lundelius et al. (1987). In the new interpretation, the Rancholabrean I of Repenning (1987) became the Irvingtonian III, whereas the Rancholabrean II became the Rancholabrean with no further subdivision (Repenning et al., 1990).

Sanders (2002) reported an astragalus assigned to *Bison* from the Ten Mile Hill Beds in Dorchester County, South Carolina. Vertebrate fossils from these beds have been dated to between approximately 240 Ka and 220 Ka on the basis of coral dates (Szabo, 1985, cited in Sanders, 2002). This record of *Bison* was employed to date the beginning of the Rancholabrean NALMA by Sanders (2002), but this interpretation has not been widely accepted to date.

Bell et al. (2004) followed Bell and Repenning (1999) in rejecting the Irvingtonian III of Repenning et al. (1990) because taxa used to define that event were found to occur in earlier faunas. Bell et al. (2004) accepted an extended Irvingtonian II that lasted to what was considered "the latest occurrence of the characteristic Irvingtonian arvicolines *Microtus paroperarius* and *Microtus meadensis*, both of which last appear in the Salamander Cave Fauna at approximately 252 Ka" (Bell et al., 2004:276). The beginning of the Rancholabrean, was defined by the first unequivocal appearance of *Bison* in North America south of 55°N latitude. This appearance was bracketed by the records of *Bison* from the American Falls Formation in Idaho between 210 ± 60 Ka and 72 ± 14 Ka, with a minimum arrival time of 160 Ka provided by the record of the genus from Jones Spring, Missouri (Bell et al., 2004). The date of approximately 240 Ka for the beginning of this age proposed by Sanders (2002) was not discussed by Bell et al. (2004) but falls within the confidence interval of the older date bracketing the fauna from American Falls.

McDonald and Morgan (1999, 2004) proposed that fossils of *Bison* are present in vertebrate faunas of late Pliocene age from Florida on the basis of horn core fragments from the Macasphalt Shell Pit (~2.6–2.2 Ma) and the Inglis 1A (~2.2–1.8 Ma) localities. If these identifications are correct, the Florida records would document a very early presence of *Bison* in North America and would force a redefinition of the Rancholabrean NALMA. However, Bell et al. (2004:285) expressed reservations about these records, including them in a discussion of "purported records [that] suffer from dubious identification, unclear stratigraphic position, or unsatisfactory chronologic control." It is further noted that should the identifications of McDonald and Morgan (1999, 2004) eventually be confirmed and/or augmented by more fossils, they would likely document an early unsuccessful immigration pulse for *Bison*, given the subsequent absence of the genus from numerous Irvingtonian localities.

An unpublished possible early record of *Bison* from the San Pedro region of Los Angeles County, California, was brought to the attention of one of us (E.S.) by the staff of the Department of Paleontology, SDSNH. This record is based on a lower molar tooth fragment (SDSNH 81193) of a large bovid comparing favorably with *Bison* and assigned to *B. antiquus*, although in fact the specimen is not sufficiently complete to be diagnostic to species. SDSNH 81193 was recovered from locality SDSNH 3246B, located south of an abandoned quarry at the former Naval Defense Fuel Reserve (M. Roeder, personal communication). Fossil mollusks collected from Pleistocene terrace deposits exposed in the east and south walls of the quarry were assigned to the Upper Bent Spring Amino Acid Assemblage Zone by Ponti (1989) and dated to about 330 Ka with amino acid ratios. The proximity of SDSNH 81193 to the dated quarry suggests that *Bison* could have been present in coastal Southern California by this time, providing a date of approximately 330 Ka for the beginning of the Rancholabrean NALMA. However, the geology of the San Pedro region is complex, other similar formations are exposed in the same region (Langenwalter, 1975), and no detailed records of the stratigraphic position and lithologic context of SDSNH 81193 are available. Locality SDSNH 3246B and the abandoned quarry were destroyed in 1988 by housing construction (Ponti, 1989), so additional sampling is not possible. The age of this specimen cannot be confirmed because the tooth was recovered away from the quarry sampled for amino acid dating, because the stratigraphic context of the tooth was not documented in detail at the time of its recovery and because the geology of the region is highly complex. The dating of SDSNH 81193 must remain uncertain.

For the purposes of this study, the recommendations of Bell et al. (2004) are followed. The beginning of the Rancholabrean NALMA is

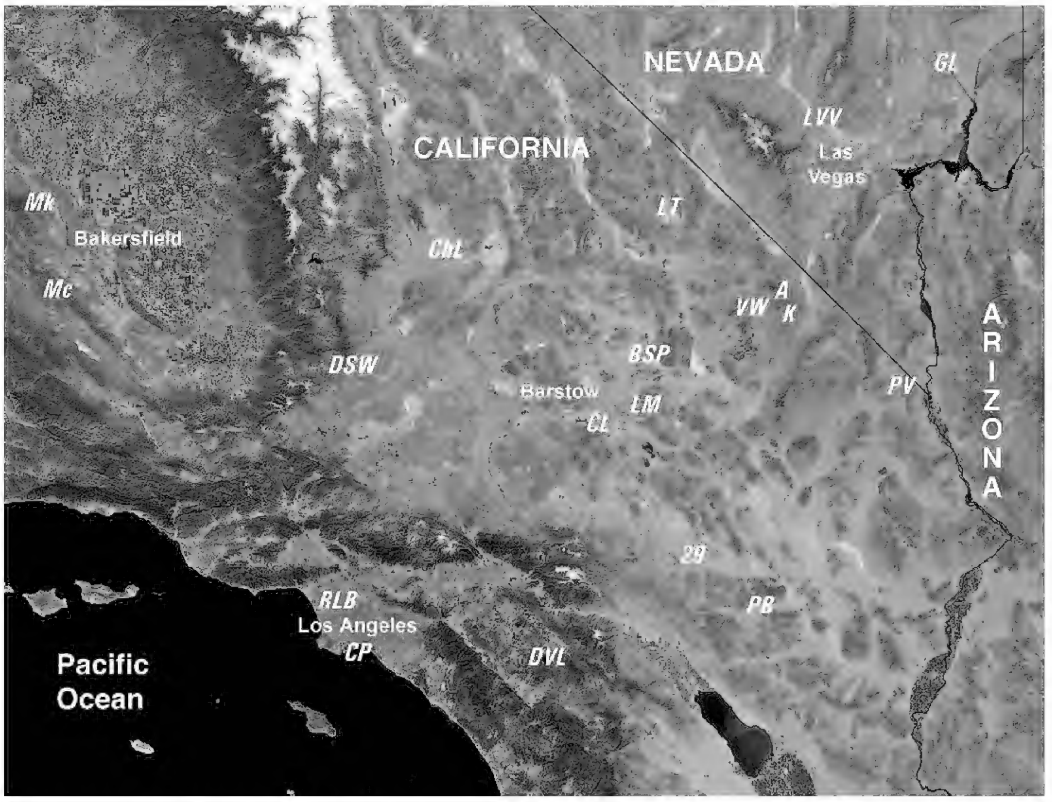

Figure 1 Map of the Mojave Desert and the surrounding region, including fossil localities discussed in the text. **ABBREVIATIONS: 29** = Twentynine Palms; **A** = Antelope Cave; **ChL** = China Lake; **CL** = Calico Lakes; **CP** = Costeau Pit; **DSW** = Dove Spring Wash; **DVL** = Diamond Valley Lake; **GL** = Glendale; **K** = Kokoweef Cave; **LLV** = Las Vegas Valley; **LM** = Lake Manix; **LT** = Lake Tecopa; **Mc** = Maricopa; **Mk** = McKittrick; PB = Pinto Basin; **PV** = Piute Valley; **RLB** = Rancho La Brea; **VW** = Valley Wells. Base map courtesy of NASA: http://veimages.gsfc.nasa.gov//5349/SWUnitedStates.A2003098.1845.250m.jpg

considered to be between 210 ± 60 Ka and about 160 Ka. However, NALMAs defined by immigrant species are inevitably time transgressive, and *Bison* arrived in some geographic regions later than others.

THE RANCHOLABREAN NORTH AMERICAN LAND MAMMAL AGE IN THE MOJAVE DESERT

Many Pleistocene vertebrate fossil sites known from the Mojave Desert have been reported to be Rancholabrean in age. Of these, some have yielded limited numbers of species, whereas others have yielded abundant microfossils but few fossils of large mammals (Harris, 1985; Heaton, 1990; Jefferson, 1991a, 1991b). Nine localities yielded faunas in which relatively abundant large mammal fossils represented multiple individuals of several (more than four) large mammal species. These localities (Fig. 1) include Bitter Springs Playa, Fort Irwin (Reynolds and Reynolds, 1994; Scott, 2000); China Lake (Davis and Panlaqui, 1978; Fortsch, 1978); Glendale (Van Devender and Tessman, 1975; Heaton, 1990); Kokoweef Cave (Reynolds et al., 1991c); Lake Manix (Jefferson, 1968, 1985, 1987); Lake Tecopa (Reynolds, 1991); the Las Vegas Valley, including Tule Springs (Simpson, 1933; Mawby, 1967; Reynolds et al., 1991b); and Valley Wells (Reynolds et al., 1991a). Not all of these localities are exclusively late Pleistocene in age; Lake Manix, for example, has a middle Pleistocene faunal component (Jefferson, 1987), whereas Lake Tecopa and Valley Wells date in part to the latest Pliocene (Reynolds et al., 1991a; Woodburne and Whistler, 1991).

The late Pleistocene faunas from the above-named localities share similar large mammal species (Table 1). The main observed difference among these faunas is the presence or absence of *Bison*. This genus is present at only China Lake, Lake Manix, and the Las Vegas Valley. Fossils of *Bison* also were identified in smaller assemblages from Dove Spring Wash (Whistler et al., 1991; Scott et al., 2001), the Twentynine Palms area

Table 2 Comparison of the size (mm) of left astragalus LACM 131119 from Dove Spring Wash with left astragali of *Bison latifrons* from American Falls and *Bison antiquus* from Rancho La Brea. Measurements taken after Von den Driesch (1976).

	Lateral length	Medial length	Distal breadth
LACM 131119	93.60	85.62	65.06
American Falls (n = 3)	102.14–104.92	94.24–97.72	68.20–70.37
Rancho La Brea (n = 89)	79.73–97.38	73.96–89.15	48.73–66.73

Specimens measured: Left astragali, *B. latifrons*, American Falls: IMNH 47001/2482, 48001/26594 P, 75002/27; left astragali, *B. antiquus*, Rancho La Brea: LACMHC Y813, Y815, Y816, Y818, Y834, Y848, Y853–Y856, Y858, Y860–Y862, Y865–Y873, Y875, Y876, Y878, Y879, Y881, Y882, Y884–Y889, Y892, Y893, Y897, Y899–Y901, Y904–Y906, Y909–Y916, Y920–Y924, Y926, Y933–Y935, Y937, Y938, Y940, Y945–Y947, Y953, Y958, Y961, Y964, Y965, Y968–Y970, Y972–Y974, Y976–Y979, Y981, Y983, Y984.

(Bacheller, 1978; Jefferson, 1992), the Piute Valley (Jefferson, 1991a), and the Pinto Basin (Jefferson, 1992). Overall, remains of *Bison* have been reported from only seven of 54 localities (13%) of presumed Rancholabrean age where large mammal fossils have been recovered on the basis of data from Harris (1985) and Jefferson (1991b). This relatively limited distribution contrasts sharply with that evinced by extinct *Bison* elsewhere in Southern California. At many localities, including Rancho La Brea (Shaw and Quinn, 1986; Stock and Harris, 1992), Diamond Valley Lake (including the Diamond and Domenigoni valleys; formerly termed the "Eastside Reservoir"; Springer and Scott, 1994; Springer et al., 1999, 2007), Costeau Pit (Miller, 1971), Maricopa (Torres, 1989), and McKittrick (Harris, 1985; Torres, 1989), fossils of *Bison* are abundant and compose a significant proportion of the large herbivore fauna.

This study was prompted by the discovery of fossils of *Bison* at Dove Spring Wash (Whistler et al., 1991; Scott et al., 2001) because a better understanding of the actual abundance and diversity of fossils of extinct *Bison* from other localities in the Mojave Desert was required to interpret correctly the significance of the new finds. However, from the outset, this task proved more difficult than it was originally supposed. No detailed specimen descriptions of fossils of *Bison* from the Mojave Desert are published, and in fact, only two published accounts (Simpson, 1933; Mawby, 1967) contain descriptions of any kind, and they both discuss fossils from the Las Vegas Valley. Simpson (1933) assigned the bison fossils from this area to *Bison* aff. *Bison occidentalis* Lucas, 1898, on the basis of two largely complete bison skulls (one illustrated with a photograph) and assorted teeth and fragments of bone. Simpson argued that the fossils belonged to a "general group" including *B. occidentalis*; *Bison crassicornis* Richardson, 1854; *Bison chaneyi* Cook, 1928; *Bison taylori* Hay and Cook, 1928; and *Bison texanus* Hay and Cook, 1928, "without resembling any one of these closely enough for specific reference" (Simpson, 1933:6). Simpson's taxonomy included many putative species that have subsequently been synonymized (see Skinner and Kaisen, 1947; Guthrie, 1970, 1990; and McDonald, 1981, for discussions). The species present in the Las Vegas Valley was characterized by its robustness; its broader frontals; and its longer, straighter horn cores relative to *B. occidentalis* (Simpson, 1933). These three characters represent essentially the entire diagnosis.

Mawby (1967) preferred an assignment of *Bison* sp. for the fossils that were recovered during excavations conducted by the Nevada State Museum, the Southwest Museum, the University of California at Berkeley, and the University of Arizona as part of the Tule Springs Expedition of 1962–1963. Fossils of *Bison* recovered during these excavations consisted of two largely complete skeletons, an adult male and a somewhat younger female (Mawby, 1967:124) from one locality, as well as isolated teeth from other sites. Mawby (1967) noted the specific assignment earlier advanced by Simpson (1933) for fossils of *Bison* from the Las Vegas Valley, further noting that Skinner and Kaisen (1947) considered these fossils to be somewhat atypical specimens of *Bison alleni* Marsh, 1877 (a species that might be of uncertain validity [Guthrie, 1970; Dalquest and Schultz, 1992] or a junior synonym of *Bison latifrons* Harlan, 1825 [McDonald, 1981]). However, the two skeletons of *Bison* recovered by the Tule Springs Expedition lacked complete skulls, which precluded the possibility of assigning the fossils to species because extinct species of *Bison* have been identified primarily on the basis of horn core morphology. No additional specimen descriptions or diagnoses were advanced by Mawby (1967), although he did present photos of a left dentary and a left metacarpal.

Other than these limited descriptions, no additional published diagnoses are available for any of the fossils of extinct *Bison* reported to date from the Mojave Desert. Published records from China Lake (Davis and Panlaqui, 1978; Fortsch, 1978), Lake Manix (Jefferson, 1987), the Pinto

Basin (Jefferson, 1992), the Piute Valley (Jefferson, 1991a) and Twentynine Palms (Bacheller, 1978; Jefferson, 1992) are all presented in faunal lists, with no description of individual specimens. One unpublished systematic account by Jefferson (1968) exists for fossils from Lake Manix, which stated that fossils recovered from Lake Manix "compare favorably with specimens of *B. antiquus* from Rancho La Brea" (Jefferson, 1968:84). Measurements presented by Jefferson (1968) of the dentition of one specimen, a partial right dentary (UCMP 310513), indicate that teeth from Lake Manix fall within the size range of teeth from Rancho La Brea. Jefferson (1968) also presented a figure of UCMP 310513, which enabled confirmation of the affinities with *Bison* of that specimen.

In the absence of published specimen descriptions, species identifications, or assessments of species abundance and diversity for large mammal faunas from the Mojave Desert, it was necessary to visit the pertinent museum collections to examine the actual fossils on which the published faunal lists were based. This research was conducted from 2001 through mid-2004.

The taxonomy of North American Pleistocene *Bison* is complicated at best, and although there is some general agreement about the broad strokes, the details are not yet resolved to the satisfaction of all workers. In the Mojave Desert, in those rare cases where fossils of *Bison* are actually assigned to species, only three species are generally employed at present: *B. antiquus*, *B. latifrons*, and *B. occidentalis*. (As noted previously, Skinner and Kaisen [1947] considered fossils from the Las Vegas Valley to represent a variant of *B. alleni*, but the validity of this species is uncertain.) This taxonomy, which conforms to that of Guthrie (1970, 1990), is employed here. Given the infrequency and fragmentary nature of most fossils of *Bison* from the Mojave Desert, no attempt is made to advance systematic or phylogenetic interpretations.

McDonald (1981) proposed that many Pleistocene *Bison* groups could be identified to the subspecific level. This interpretation resembles the systematics of extant *Bison*, which are frequently separated at the subspecific level (Nowak, 1991). Plains bison (*Bison bison bison* Linnaeus, 1758) are morphologically distinct from woodland bison (*Bison bison athabascae* Rhoads, 1897), they are geographically isolated populations, and they are demonstrably interfertile when they come into contact. For fossil species, although morphologic distinctiveness can be demonstrated, interfertility cannot. Furthermore, the use of subspecies implies a level of phylogenetic precision that the very nature of the fossil record does not support, and we do not consider fossil subspecies to be verifiable in practice. Whereas McDonald (1981) preferred the trinomial *B. antiquus antiquus* for the smaller and more common of Southern California's late Pleistocene *Bison* species, we refer to this animal as *B. antiquus* with no subspecific refinement.

RESULTS

Results are organized by locality in alphabetic order. Amended diagnoses for reidentified specimens are provided only where necessary.

China Lake

PREVIOUS IDENTIFICATIONS. *Bison* sp. (Fortsch, 1978); *Bison* cf. *B. antiquus* (Davis and Panlaqui, 1978); *B. antiquus antiquus* (McDonald, 1981).

REFERRED MATERIAL. LACM 27841, partial right dentary with p4–m3; LACM 27843 or 29599, partial ramus of right dentary with fragments of m1–3; LACM 29015, skull with broken horn cores (presently on display at MM). All of these fossils, recovered from locality LACM 7013, are listed in the collections of the LACM as '*Bison* cf. *B. antiquus*'. Additionally, 96 specimens from this locality are assigned to '*Bison* sp.': LACM 25154, portions of right metacarpal III and IV; 26586, second phalanx; 26589, fragment of anteroposterior portion of right metacarpal III and IV; 26606, fragment of left calcaneum; 26608, second phalanx; 26609, body of anterior thoracic vertebra lacking neural spine; 26622, fragment of head of ?left femur; 26625, fragment of right side of anterior thoracic vertebra; 26630, centrum of anterior thoracic vertebra; 26640, fragmentary anteromedial portion of left dentary, with part of symphysis; 26641, ungual phalanx; 26643, distal epiphysis of left tibia; 26648, distal articulation of left tibia, probably juvenile; 26655, fragment of distal articulation of left radius; 26658, right occipital condyle; 26667, second phalanx; 26668, ungual phalanx; 26669, second phalanx; 26670, ungual phalanx (note: the previous four specimens might be from one individual); 26674, anterior fragment of centrum of thoracic vertebra; 26679 and 29115, distal metapodial portion (in two pieces, catalogued separately and later glued together); 26681, fragment of distal articulation of left tibia; 26690, broken proximal epiphysis of first phalanx; 26695, left lunar; 26707, centrum of thoracic vertebra; 26768, partial left unciform; 26857, partial right unciform; 27013, partial thoracic vertebra, juvenile; 27015, partial right scaphoid; 27016, fragment of distal right humerus; 27020, portion of thoracic vertebra; 27034, fragment of distal articulation of ulnar portion of left radius–ulna; 27035, left scaphoid; 27036, left lunar; 27037, left cuneiform; 27412, right metacarpal V; 27413, distal metapodial; 27485, proximal first phalanx; 27486, fragment of

ischial portion of right acetabulum; 27488, proximal fragment of ungual phalanx; 27501, fragments of ungual phalanx; 27609, fragment of ungual phalanx; 27611, fragment of zygomatic process of left temporal; 27620, portion of distal metapodial (possibly left metacarpal III and IV); 27622, right postzygapophysis of lumbar vertebra ?V; 27628, second phalanx; 27632, fragment of medial side of distal articulation of first phalanx; 27634, horn core fragments; 27639, fragment of ?left frontal with horn core fragment; 27645, fragment of left ectocuneiform; 27651, fragment of anterior face of proximal portion of left radius; 27661, fragment of proximal articulation, anterior face, right metacarpal III and IV; 27662, lateral fragment of proximal right tibia; 27663, fragment of left naviculocuboid; 27668, fragment of ungual phalanx; 27673, fragment of proximal articulation of first phalanx; 27741, horn core fragments; 27752, partial second phalanx; 27754, portion of centrum of sacrum; 27761, horn core fragment; 27770, partial second phalanx; 27771, partial right mesoectocuneiform, possibly juvenile or subadult; 27806, fragment of right calcaneum; 27811, partial right mesoectocuneiform; 27823, associated skull fragments; 27832, partial left ilium; 27833, partial neural spine and neural arch with zygapophyses of posterior thoracic vertebra; 27834, distal epiphysis of right metacarpal IV; 28655, partial ungual phalanx; 28661, odontoid process of axis vertebra; 28663, distal portion of right fibula; 28678, associated fragments of partial cranium including horn core; 28692, partial right occipital condyle; 28705, fragment of odontoid process of axis vertebra; 28709, left naviculocuboid; 28710, partial right magnum; 28721, fragment of laterodistal left calcaneum; 28726, fragment of medioproximal articulation of left radius; 28731, fragment of laterodistal portion of right calcaneum; 28733, partial ungual phalanx; 28761, partial right cuneiform; 28762, fragment of mesiodistal right humerus; 28777, fragment of anterior portion of right ulna; 28789, fragment of right temporal with portion of the auditory canal; 28806, fragment of left temporal with portion of the auditory canal; 28828, fragment of anterior right ala of atlas; 28831, second phalanx; 28841, fragment of inferior puboischiatic symphysis; 28844, fragment of posterocentral portion of left radius–ulna; 28852, horn core fragments; 28858, partial right entocuneiform; 28868, partial left entocuneiform; 28930, partial left pisiform; 28934, partial right mesoectocuneiform; 28944, partial right fibula; and 28951, articular portion of left dentary with condyloid and coronoid processes. Twenty-three fossils from China Lake locality LACM 7013 are assigned to '?*Bison*' or 'cf. *Bison*', including LACM 26618, enamel fragment, possibly from posterior m1; 26619, fragment of head of humerus; 26657, distal metapodial fragment; 26663, partial left postzygapophysis of cervical vertebra; 26665, fragment of right scaphoid; 26612, enamel fragment, labial side of left P4; 26691, fragment of lateral side of distal left tibia; 26873, fragment of left astragalus; 26882, fragment of lateral side of proximal articulation of right tibia; 27011, fragment of head of humerus; 27492, fragment of right squamosal with part of foramen ovale; 27502, fragments of glenoid fossa of ?left scapula; 27630, atlas fragment; 27636, fragment of neural arch and postzygapophyses, possibly from anterior lumbar vertebra; 27652, fragments of thoracic vertebra; 27742, tooth fragments; 27743, fragment of second phalanx; 27755, fragment of left naviculocuboid; 28669, fragment of mediodistal articulation of humerus; 28817, fragment of lateral side of proximal phalanx; 28915, fragment of lateral side of distal left radius–ulna; 28932, partial metapodial sesamoid; and 28952, skull fragments. All of these specimens were re-examined for this report. (Additional specimens in the collections of the LACM from China Lake that were assigned to *Bison*, but for which the identifications could not be confirmed, are not included herein.)

AMENDED IDENTIFICATION. *Bison* cf. *B. antiquus*. (Fossils previously assigned to *Bison* sp., ?*Bison*, or cf. *Bison* retain those identifications with no additional refinements.)

DISCUSSION. These fossils are relatively abundant, although extremely fragmentary in most cases. Acquisition of meaningful, repeatable measurements from these fossils is not possible, because of heavy breakage and extensive abrasion and wear. However, those few fossils that are more complete appear to resemble *B. antiquus* in size and morphology and likely represent this species, although the 'sp. cf.' designation is best retained until more and better material is recovered from the area. Of the more complete specimens, LACM 29015, a partial skull from locality LACM 7013 on display at the MM, exhibits broad frontals and small horn cores that project straight out to the sides. The small size of the horn cores precludes assignment to any of the known long-horned species of *Bison* (e.g., *B. latifrons* or *Bison alaskensis* Rhoads, 1897), whereas the straight lateral projection is reminiscent of *B. antiquus*. In contrast, horn cores of *B. occidentalis* and extant *B. bison* project both laterally and caudally from the frontal, resulting in a somewhat "swept back" appearance (Dalquest and Schultz, 1992). LACM 29015 is likely best assigned to *B. antiquus*; however, because the fossil was not available for measurement at the time of this study, we retain the "sp. cf." designation.

All other fossils listed above were examined directly and confirmed to belong to a *B. antiquus*–sized species of *Bison*. Some of these

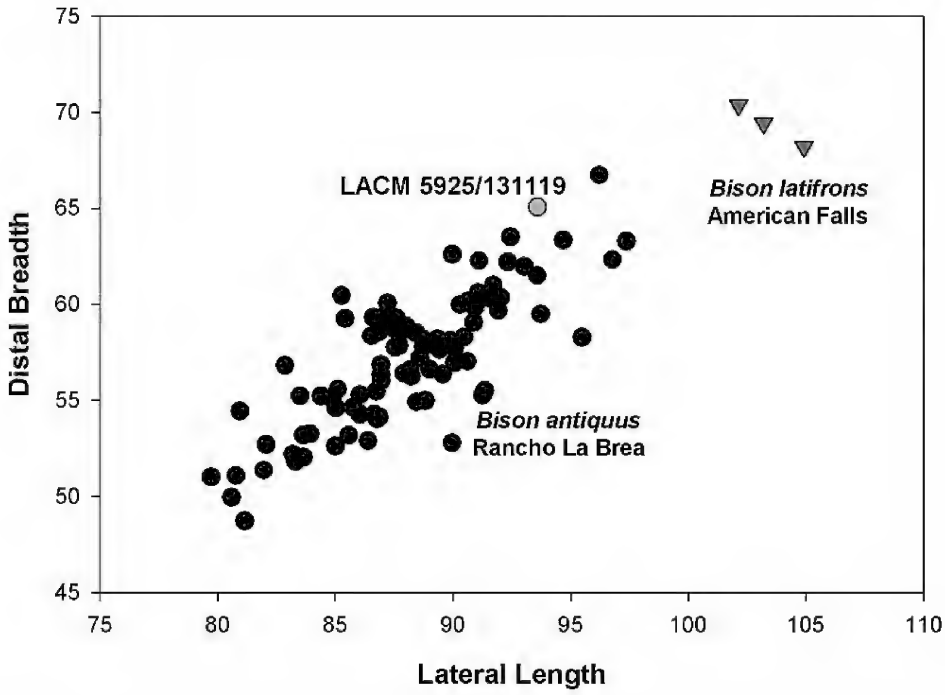

Figure 2 Bivariate graph comparing astragalus LACM 131119 from Dove Spring Wash (*Bison antiquus*) with astragali of *B. antiquus* from Rancho La Brea and *Bison latifrons* from American Falls.

specimens, too, show morphological affinities with *B. antiquus*. For example, specimen LACM 28678 consists of broken portions of a cranium including a slender horn core. This horn core is far less massive in appearance than one would anticipate for the larger, long-horned species of extinct *Bison* (e.g., *B. latifrons*), but it is similar in size and morphology to comparable elements from Rancho La Brea (Fig. 3). Furthermore, although it is broken both basally and distally, this horn core appears to project laterally and horizontally from the frontal, rather than sweeping caudally as in *B. occidentalis* and *B. bison* (Fig. 3).

Dove Spring Wash

PREVIOUS IDENTIFICATION. *Bison antiquus* (Whistler et al., 1991; Scott et al., 2001).

REFERRED MATERIAL. LACM 5924/131124, fragment of proximal right metatarsal; LACM 5924/131125, tooth fragment; LACM 5924/131133, left p4; LACM 5924/131134, distal metapodial fragment; LACM 5925/131139, partial skeleton including left astragalus (LACM 5925/131119), left malleolus (LACM 5925/131120), associated right P2–4, M1 (LACM 5925/131121), and other batch-catalogued skeletal elements, including vertebrae, ribs, and a distal left tibia that articulates perfectly with LACM 5925/131119 and LACM 5925/131120 (LACM 5925/131122).

DISCUSSION. These fossils and their context will be described more fully elsewhere. No complete horn cores were recovered, which renders accurate assignment to species somewhat problematic (after Skinner and Kaisen, 1947; McDonald, 1981). However, linear measurements of the astragalus LACM 131119, from locality LACM 5925, fall into the upper end of the size range of *B. antiquus* from Rancho La Brea, on the basis of both published data (Miller and Brotherson, 1979) and measurements acquired for this study (Table 2). Linear measurements of this specimen fall below the size range of astragali of adult male *B. latifrons* from the American Falls Reservoir in Idaho on the basis of measurements acquired from the IMNH (Table 2, Fig. 2). Linear discriminant analysis of all measurements indicates that LACM 131119 is better referred to *B. antiquus* (92% probability) than to *B. latifrons* (8% probability).

Lake Manix

PREVIOUS IDENTIFICATION. *Bison* cf. *B. antiquus* (Jefferson, 1968, 1987).

REFERRED MATERIAL. UCMP 310513, partial right dentary with p2–4 and fragments of m1; UCMP 310689, right postzygapophysis

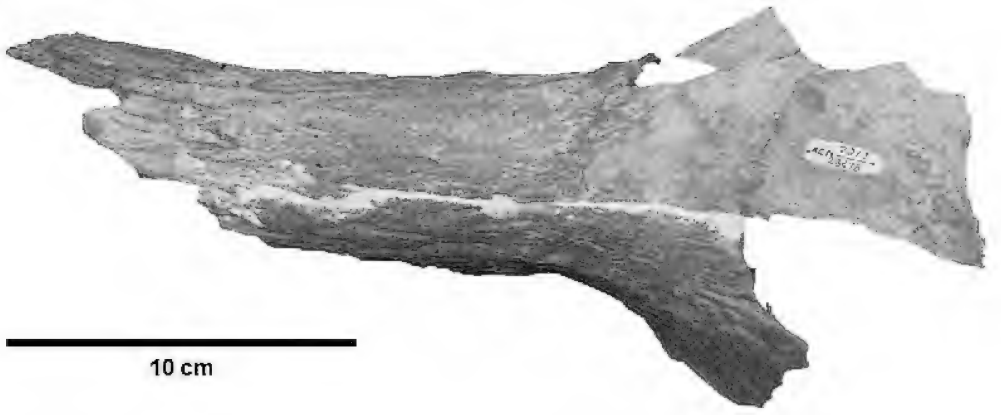

Figure 3 *Bison* cf. *B. antiquus*, LACM 28678, right horn core from China Lake, California, dorsal view.

fragment of lumbar vertebra; UCMP 310690, broken first sacral vertebra with anterior centrum and left prezygapophysis; UCMP 314667, partial centrum of first thoracic vertebra; UCMP 314677, broken third cervical vertebra; LACM 24494, broken prezygapophysis of lumbar vertebra.

EMENDED IDENTIFICATIONS. *Camelops* sp. (UCMP 310690); cf. *Camelops* sp. (UCMP 314677, LACM 24494); Camelidae, small (UCMP 314667); *Bison* cf. *B. antiquus* (UCMP 310513); Artiodactyla, large (UCMP 310689).

DISCUSSION. UCMP 310513 is a partial right dentary that, as noted by Jefferson (1968), conforms well in both size and morphology with comparable elements of *B. antiquus* from Rancho La Brea (Fig. 4). Although the taxonomy of Pleistocene *Bison* is generally based on the morphology of the horn cores, no such element is known from Lake Manix. Nevertheless, the similarities between UCMP 310513 and dentaries of *B. antiquus* from Rancho La Brea merit assignment of the Lake Manix specimen to this species. As with the China Lake fossils, retention of Jefferson's (1968) 'sp. cf.' designation is recommended until more diagnostic fossils are recovered from the area.

In contrast, none of the remaining fossils from Lake Manix that previously were assigned to *Bison* can be confirmed to belong to this taxon. This is important because the stratigraphic position and inferred geologic age of these specimens have powerful implications for understanding the biostratigraphy of Lake Manix and the Mojave Desert as a whole. If these fossils were indeed *Bison*, they would represent the earliest confirmed occurrence of this taxon in North America south of the glacial ice, and they could be employed to define the beginning of the Rancholabrean NALMA in the western United States. Considering the ramifications of these new identifications, some detail is warranted in the following discussion.

The postzygapophysis fragment UCMP 310689 exhibits an S-shaped morphology in transverse section, and it is clearly from a large artiodactyl. UCMP 310690, from the same locality as UCMP 310689, possesses a prezygapophysis with a similar morphology. According to G.T. Jefferson (personal communication), the S-shaped zygapophyses in UCMP 310689 and 310690 suggested affinity with *Bison* because this feature is common in that taxon. A photograph of UCMP 310689 was supplied to J.R. McDonald, a specialist in fossil bison who confirmed this identification (G.T. Jefferson, personal communication). However, similar S-shaped zygapophyses are not restricted to *Bison* and can also be seen in other artiodactyls, including *Camelops*. UCMP 310689 is therefore a large artiodactyl, but it is not otherwise diagnostic to genus.

Although UCMP 310689 and 310690 cannot be directly articulated, because they are from

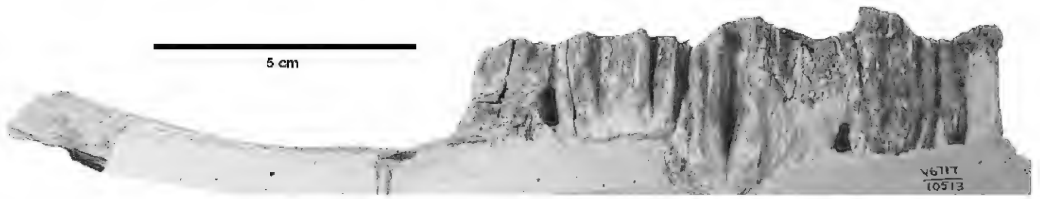

Figure 4 *Bison* cf. *B. antiquus*, UCMP 310513, right dentary fragment from Lake Manix, lingual view. Photo by Pennilyn Higgins, Florida Museum of Natural History. Used with permission.

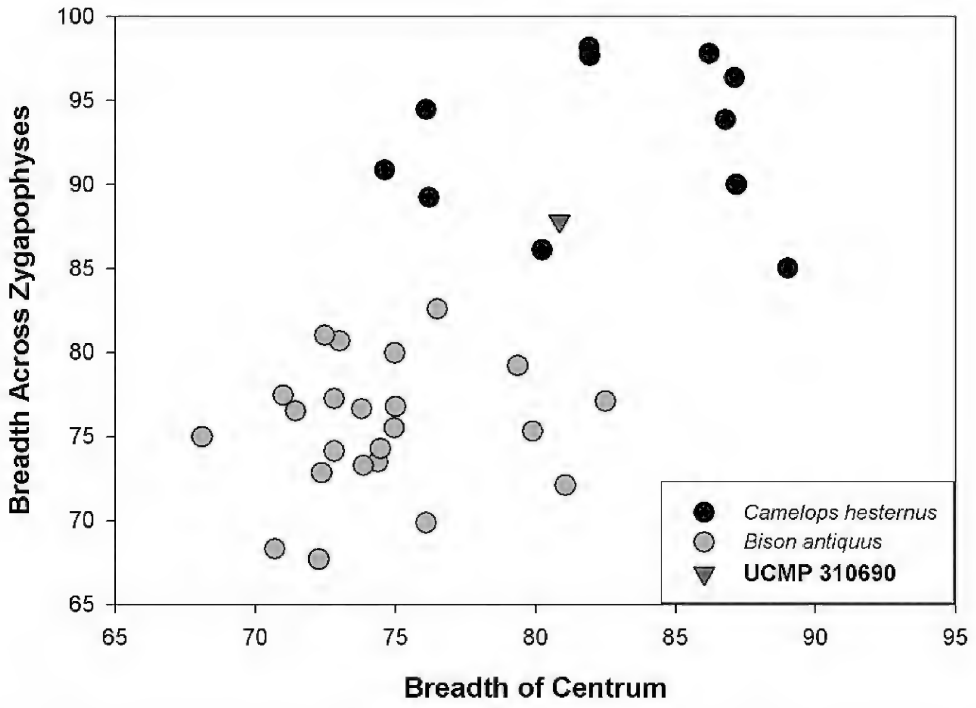

Figure 5 Three-dimensional graphic plot of measurements of UCMP 310690 from Lake Manix against first sacral vertebrae of *Camelops hesternus* and *Bison antiquus* from Rancho La Brea.

opposite sides of the body, their geographic proximity and close similarity in size and shape suggest that these two bones might come from the same individual. UCMP 310690 is diagnostic; in its size (Fig. 5), the conformation of the prezygapophyses, the relative position of the prezygapophyses to the centrum, the distance between the prezygapophyses, the shape and proportions of the centrum, and the cranial projection of the alae, UCMP 310690 resembles specimens of *Camelops hesternus* from Rancho La Brea very closely, whereas it differs markedly from *B. antiquus* from that site (Fig. 6). UCMP 310690 is therefore assigned to *Camelops* rather than to *Bison*. Because UCMP 310689 is very likely from the same individual as UCMP 310690 and exhibits a morphology consistent with *Camelops*, it likely belongs in this taxon, but given the very fragmentary nature of UCMP 310689, and considering that it cannot presently be proven to be the same individual as UCMP 310690, a more conservative assignment to Artiodactyla (large) is used.

Specimens UCMP 314667 and 314677, originally identified as '*Tanupolama*' (= *Hemiauchenia*) and *Camelops*, respectively, on specimen labels, had both been re-identified as *Bison*. In both cases, the original identifications were more accurate. UCMP 314667 differs from *Bison* in its smaller size as well as in the shape of its centrum, which in anterior or cranial view is dorsally broad but tapers ventrad; in *Bison*, the centrum is less broad dorsally and does not taper ventrad. There is also the ventral remnant of a pronounced invagination or groove posterior to the right transverse process of UCMP 314667 that closely matches a similar groove seen in the first thoracic vertebrae of *Camelops* and *Hemiauchenia* Gervais and Ameghino, 1880, but it is too extensively developed anteroposteriorly to be comparable to the small foramina present in this region of thoracic vertebrae of *Bison*. Considering the fragmentary nature of UCMP 314667, we prefer a conservative assignment to a small species of undetermined Camelidae.

UCMP 314677 is larger than UCMP 314667 and is similar in size to the third cervical vertebrae of both *Camelops* and *Bison*. However, the ventral portion of the neural canal of UCMP 314677 is transversely quite narrow, very much like the canals present in anterior thoracic vertebrae of *Camelops* and much less broad than those seen in *Bison*. UCMP 314677 also exhibits a flattened anterior centrum with a cranially projecting ventral edge that closely resembles *Camelops* but differs from the more convex condition observed in *Bison*. Finally, although it is broken caudally, the body of the centrum

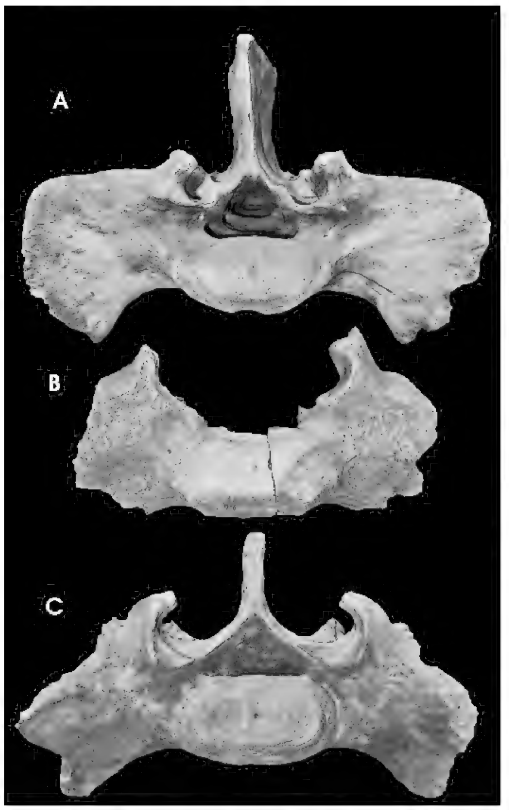

Figure 6 Visual comparison between first sacral vertebrae of *Bison antiquus* from Rancho La Brea [**A**], UCMP 310690 from Lake Manix [**B**], and *Camelops hesternus* from Rancho La Brea [**C**], anterior view. Note the size and shape of the centrum, the distance between the prezygapophyses, and the orientation of the alae.

appears to extend caudad in a relatively straight line as in *Camelops*, whereas in *Bison*, the centrum body projects ventrad toward the caudal end. The original identification in the collections of UCR listed this fossil as *Camelops*, and we concur with this assignment.

One other previously unpublished specimen, LACM 24494 from locality LACM 1093, is identified in the collections of the LACM as *Bison* sp. This specimen also closely resembles *Camelops*. Of particular interest in advancing this determination was a thin bony ridge, located lateral to the neural canal beneath the prezygapophysis, that extends smoothly from the base of the prezygapophysis onto the anterior or cranial edge of the transverse processes. This feature matches one observed on lumbar vertebrae of *Camelops* from Rancho La Brea, but it differs from homologous elements of *Bison*. For this reason, but once again considering the fragmentary nature of the fossil, LACM 24494 is assigned to cf. *Camelops*.

Las Vegas Valley

PREVIOUS IDENTIFICATIONS. *Bison* aff. *occidentalis* (Simpson, 1933); *B. alleni* (Skinner and Kaisen, 1947); *Bison* sp. (Mawby, 1967); *B. antiquus antiquus* (McDonald, 1981).

REFERRED MATERIAL. UCMP V-6243/64645, right metacarpal; UCMP V-6243/64646, left metacarpal; V-6243/64683, right astragalus; V-6243/64685, left magnum; V-6243/64686, right magnum; V-6243/64687, left magnum.

EMENDED IDENTIFICATION. *Bison* cf. *B. antiquus*.

DISCUSSION. For the purposes of this study, two "voucher" metacarpals (UCMP V-6243/64645 and V-6243/64646) were selected for examination. These specimens are both relatively complete, permitting measurements to be acquired. The size of these specimens falls within the range of *B. antiquus* from Folsom and Rancho La Brea (Fig. 7), although UCMP V6243/64646, listed in the collections of the UCMP as a male from Tule Springs Site #2, also falls close to the low end of the size range for *B. latifrons* from American Falls Reservoir. Associated postcrania from Tule Springs also fall within the size ranges of like elements of *B. antiquus*. In the absence of complete and fully diagnostic horn cores, the fossils from the Las Vegas Valley are conservatively assigned to *Bison* sp. cf. *B. antiquus*.

Pinto Basin

PREVIOUS IDENTIFICATION. *Bison* sp. (Jefferson, 1992).

REFERRED MATERIAL. LACM 47255, broken fragment of the supraglenoid tubercle with a portion of the coracoid process of the right scapula.

EMENDED IDENTIFICATION. *Camelops* sp.

DISCUSSION. Published reports discussing the Pleistocene vertebrate fossil assemblage from the Pinto Basin in Joshua Tree National Park, Riverside County, California, offer contradictory views regarding the presence of *Bison*. Jefferson (1991a, 1991b) presented a faunal list for the site that did not include *Bison*, but a subsequent report (Jefferson, 1992) reported that *Bison* sp. was a "common" Pleistocene taxon from the region. Only one fossil fragment was located in museum collections on which this record might be based. This fossil, LACM 47255 from locality LACM 3414, was identified in the collections of the LACM as a "fragment of right tuber of calcaneum" of *?Bison*. Examination of this specimen by one of us (E.S.) during an ongoing study of fossils from the Pinto Basin (Scott et al., 2006) confirmed that the cortical bone was too thin and the cancellous bone too porous for the fossil to be a calcaneum of *Bison*.

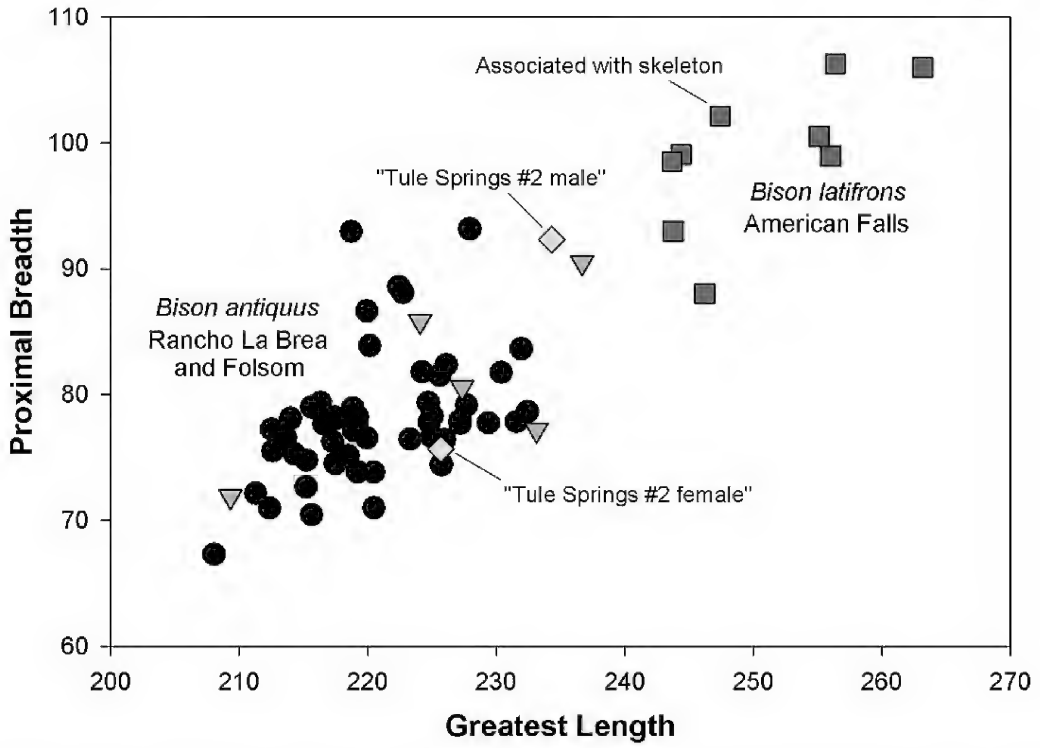

Figure 7 Bivariate graph comparing metacarpals UCMP V-6243/64645 ("Tule Springs #2 female") and V-6243/64646 ("Tule Springs #2 male") from Tule Springs with metacarpals of *Bison antiquus* from Folsom and Rancho La Brea and *Bison latifrons* from American Falls. **ABBREVIATIONS: circles** = Rancho La Brea; **squares** = American Falls; **triangles** = Folsom; **diamonds** = Tule Springs. Only one of the metacarpi from American Falls is associated with a skeleton that includes diagnostic horn cores; this specimen is noted.

Comparison with fossils from Diamond Valley Lake at the SBCM and from Rancho La Brea at the GCPM confirmed that the fossil closely resembled a fragment of proximal scapula of *C. hesternus* (Leidy, 1854) (Fig. 8). Assignment to species is not warranted because of the fragmentary nature of the fossil. However, because the fossils from the Pinto Basin are Pleistocene in age on the basis of the presence of *Mammuthus* (Scott et al., 2006), the size and morphology of LACM 47255 indicate that the fossil is best referred to *Camelops*.

Piute Valley

PREVIOUS IDENTIFICATION. *Bison* cf. *B. latifrons* (Jefferson, 1971).

REFERRED MATERIAL. SBCM A500-1309, broken semilunar notch of left ulna; SBCM A500-1310, fragmentary right ischium.

EMENDED IDENTIFICATION. Bovidae, large (SBCM A500-1309); *Equus* sp., large (SBCM A500-1310).

DISCUSSION. Fossils from the Piute Valley were not described previously, but they were reported in faunal lists (Jefferson, 1991a). We found only two fossils from the region previously attributed to *Bison*, both in the collections of the SBCM. Specimen A500-1309 from locality SBCM 1.28.1 was labeled *Bison* cf. *B. latifrons*. The specimen exhibits a relatively narrow, straight anterior edge of the olecranon process that resembles *Bison* and differs from both *Equus* (which has a narrow but strongly curved anterior edge on the olecranon) and *Camelops* (which exhibits a broad, straight anterior edge). The articular surface of A500-1309 also resembles homologous elements of *B. antiquus* from Rancho La Brea in both size and morphology.

Given the fragmentary nature of this specimen, and considering that other large bovids were also present in the Great Basin during the late Pleistocene (Heaton, 1990) and might have been present in the Mojave Desert as well (G.T. Jefferson, personal communication), A500-1309 is best interpreted conservatively as a large species of undetermined bovid. Additional, more diagnostic fossils of extinct *Bison* will need to be recovered from the Piute Valley before this record can be confirmed.

In contrast, specimen A500-1310 from locality SBCM 1.28.1, which was labeled as a fragment of

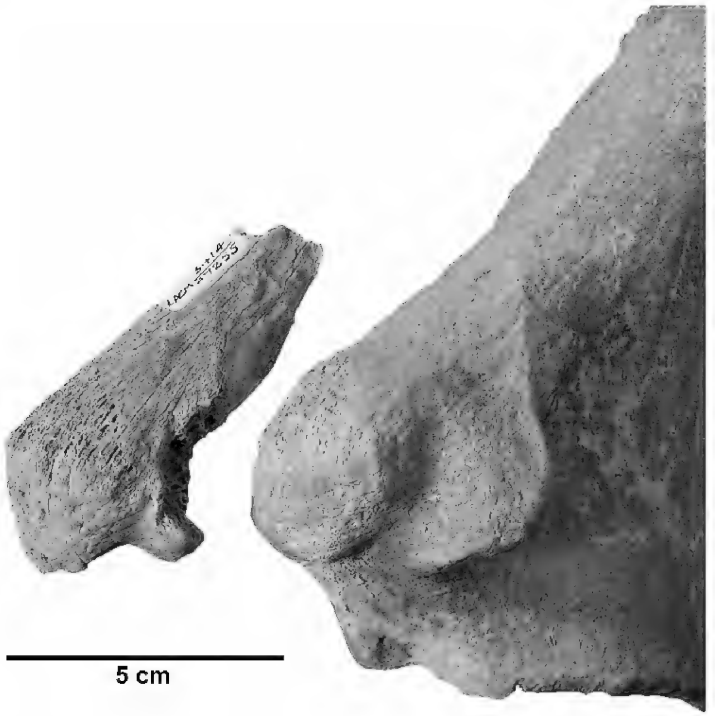

Figure 8 **Left:** LACM 47255, broken fragment of the supraglenoid tubercle with a portion of the coracoid process of the right scapula, previously assigned to *Bison* and here referred to *Camelops*. **Right:** SBCM L2726-17737, proximal right scapula of *Camelops hesternus* from Diamond Valley Lake.

left ischium attributed to *Bison* cf. *B. latifrons*, is actually a fragmentary right ischium of large horse (*Equus* sp.). The specimen includes a portion of the rim of the obturator foramen that is curved more tightly than in *Bison* but that closely resembles the curvature seen in ischia of *Equus*. The fragment is broken laterally, but nevertheless appears more broadly triangular in cross section, as in *Equus*, than narrowly ovular and tapered posteriorly as in *Bison*. Finally, the origin of the m. quadratus femoris, a small bony prominence or ridge on the ventral face of ischia of *Bison* just lateral to the caudal ventral edge of the obturator foramen, is absent on A500-1310; this feature is also lacking in *Equus*.

Twentynine Palms

PREVIOUS IDENTIFICATIONS. *Bison* cf. *B. antiquus* (Bacheller, 1978; Jefferson, 1991a).

REFERRED MATERIAL. LACM 51407, weathered left magnum; SBCM A500-1128, fragments of right dentary including partial ascending ramus with coronoid process and anterior diastema portion with broken root of p3.

AMENDED IDENTIFICATION. *Bison* sp. (very large), possibly *B. latifrons* or *B. alaskensis* (LACM 51407); *Camelops* sp. (SBCM A500-1128).

DISCUSSION. Fossils assigned to *Bison* have been reported from Surprise Springs and from the Twentynine Palms Gravel Pit in the Twentynine Palms area. Specimen LACM 51407 from Surprise Springs locality LACM 3350 exhibits a morphology resembling *Bison* (Fig. 9) but differs from other Pleistocene bovids such as *Bootherium* Leidy, 1852. Viewed ventrally, the lateral posterior portion of the metacarpal facet is relatively

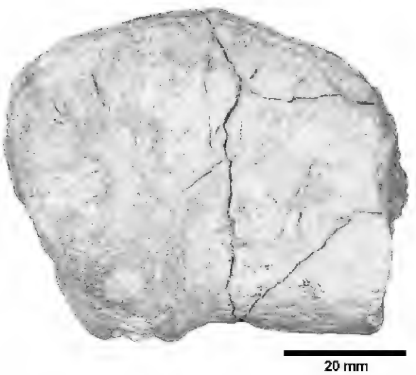

Figure 9 *Bison* sp. (very large), LACM 51407, weathered left magnum of from Twentynine Palms, distal view.

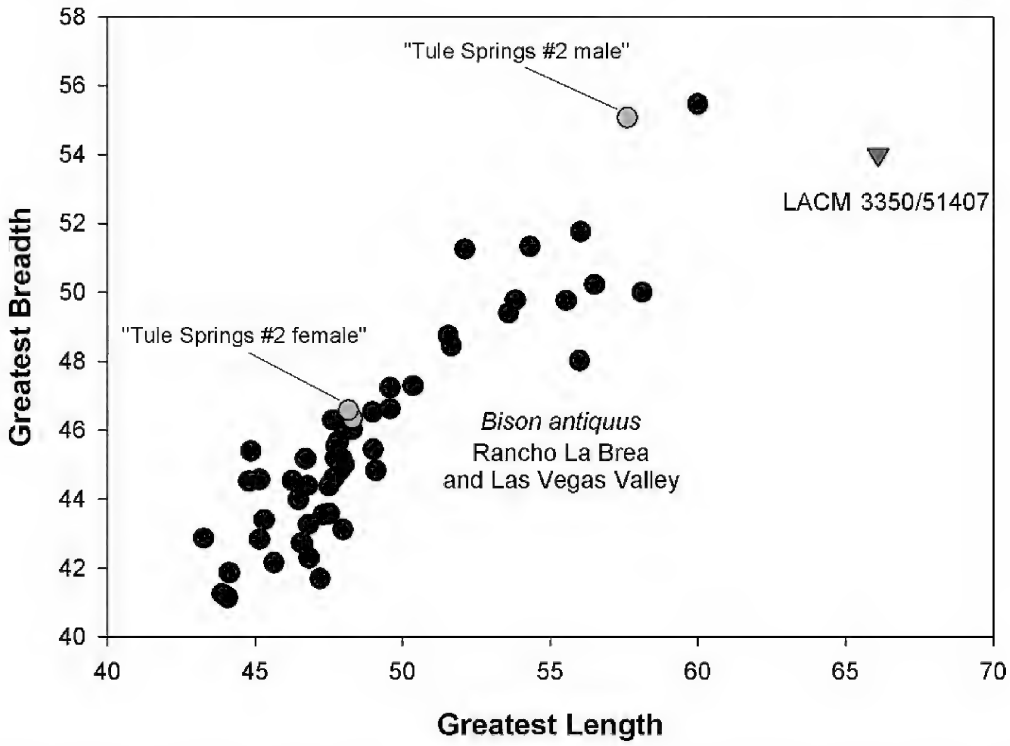

Figure 10 Bivariate graph comparing measurements of magnum LACM 51407 from Twentynine Palms with measurements of like elements of *Bison antiquus* from Rancho La Brea. **ABBREVIATION: dark circles** = Rancho La Brea; **light circles** = Tule Springs; **triangle** = Twentynine Palms.

flat, as seen in *Bison* but differing from the more transversely concave surface observed in *Bootherium*. The lateral edge of the scaphoid facet extends posteriad in a relatively straight line and projects to near the metacarpal facet, as in *Bison*, rather than curving mediad away from the metacarpal facet as in *Bootherium*. The lunar facet is relatively broad and forms a shelf, as seen in *Bison*, rather than narrow and forming a ridge as in *Bootherium*. The relatively greater breadth of the lunar facet in LACM 51407 is also clearly visible in proximal view (Fig. 9), as is the strong curvature of the dorsal face of the bone that typifies *Bison*, but differs from *Bootherium*. Given the observed morphology, LACM 51407 is assigned to *Bison*. The specimen is significantly larger than comparable elements of *B. antiquus* from Rancho La Brea (Fig. 10) and cannot be assigned to that species. On the basis of the observed morphology and size, LACM 51407 likely represents a very large species of *Bison* (e.g., *B. latifrons*, or another long-horned species, *B. alaskensis*).

Specimen SBCM A500-1128 from locality SBCM 1.86.1 at the Twentynine Palms Gravel Pit consists of five fragments of a right dentary. The coronoid process of this dentary is tall and gently curved anteroposteriorly, very much like the morphology observed in *Camelops* and unlike the shorter, less curved, triangular processes seen in *Bison*. The anterior diastema portion also resembles *Camelops*. SBCM A500-1128 is, therefore, assigned to that genus.

Jefferson (1991a) reported *Bison* from the Twentynine Palms Gravel Pit, presumably on the basis of the fossil from SBCM 1.86.1. A subsequent publication by this author stated that "the presence of *Bison* has not been confirmed from Campbell Hill or the Twentynine Palms Gravel Pit localities" (Jefferson, 1992:44). This study confirms the presence of fossils of *Bison* only from the Surprise Springs site.

DISCUSSION

AGE AND DISTRIBUTION OF *BISON*

The observed pattern of distribution of extinct *Bison* in late Pleistocene faunas of the Mojave Desert is unusual, particularly when compared with the distributions of other large herbivores. As stated previously, fossils of *Mammuthus* spp., *Equus* spp., *Camelops* spp., and *Hemiauchenia* sp. are relatively common in late Pleistocene assemblages throughout the Mojave Desert (Table 1), although as observed by Jefferson (1992),

these taxa as well as *Bison* are more frequent in lowland assemblages. *Bison* is decidedly underrepresented in the region, even though *Bison* was clearly compatible with mammoths, horses, and camels throughout most of Southern California, as evidenced by assemblages from Rancho La Brea (Shaw and Quinn, 1986; Stock and Harris, 1992), Diamond Valley Lake (Springer and Scott, 1994; Springer et al., 1999, 2007), Costeau Pit (Miller, 1971), Maricopa (Torres, 1989), and McKittrick (Harris, 1985; Torres, 1989), to name just a few localities.

This review shows that, with one possible exception (the record from Twentynine Palms; see later), all of the confirmed records of *Bison* from the Mojave Desert are geologically young. For example, UCMP 310513 from Lake Manix was recovered from Unit D of the Manix Formation (Jefferson, 1968) between dated shell beds and was therefore determined to be between approximately 35 and 19 Ka (Jefferson, 1985). Vertebrate fossils including *Bison* from China Lake were recovered from three localities: LACM 3659, 7013, and 7262. Of these, LACM 7013 was by far the most productive, primarily because of its size (11 km^2) and because it was the most extensively worked of the three localities (Fortsch, 1978). All of the fossils of *Bison* from China Lake discussed herein were recovered from this locality. Mammoth (*Mammuthus*) tusk portions from LACM 7013 are dated to 18,600 ± 450 BP (Davis and Panlaqui, 1978).

The partial skeleton of *B. antiquus* from Dove Spring Wash is directly dated at 16,860 ± 1,175 BP (Scott et al., 2001), and it is therefore presently the best dated record of *B. antiquus* from the Mojave Desert. Additional fossils of *Bison* also were recovered from an older sedimentary unit at Dove Spring Wash; radiometric dating of tooth fragments of *Mammuthus* from this unit yielded an age of 19,190 ± 410 BP (Scott et al., 2001).

Excavations conducted in the mid-1990s at Tule Springs and the Las Vegas Valley by the SBCM, and more recently beginning in 2002 and continuing to the present, have recovered fossil remains of *Bison* in association with other megafaunal remains from Units B_2 and E_1 and possibly Unit D of the Las Vegas Formation; these fossils are presently under study (Springer et al., 2006). Unit B_2 has been tentatively correlated with the penultimate deep-lake episode in Death Valley (~190 Ka and ~140 Ka; Ku et al., 1998; Lowenstein et al., 1999) and isotope Stage 6 at Devils Hole (186 Ka to >130 Ka; Winograd et al., 1992, 1997) by Quade et al. (2003). More recently, Page et al. (2005:3) reported thermoluminescence dates from Unit B_2 between 144 Ka and 89 Ka. Mollusc shells from the middle of Unit D have previously been dated to 22,600 ± 550 BP, whereas shells from the base of Unit D date to 31,300 ± 2,500 BP (Haynes, 1967:73), although both of these dates were interpreted to "probably [be] 1,000 years too old." More recently acquired ^{14}C dates for exposures of this unit at Corn Creek Springs, northwest of Tule Springs, range from 19,380 ± 110 to 17,730 ± 90 BP (Quade et al., 2003). Unit E_1 has yielded ^{14}C dates between nearly 15 Ka and 11.5 Ka at Tule Springs, as well as ^{14}C dates ranging from 14,530 ± 80 BP to 11,700 ± 250 BP at Corn Creek Springs to the northwest (Haynes, 1967; Brennan and Quade, 1997; Quade et al., 2003; Springer et al., 2006). A radiocarbon (^{14}C) date of 14,780 ± 40 BP recently reported (Springer et al., 2006) is the oldest for this unit.

De Narvaez (1995) reported fossils of *Bison* from Gilcrease Ranch in the Las Vegas Valley northwest of the Tule Springs sites from deposits that conform in part to the stratigraphy outlined by Haynes (1967). At this site, Gilcrease Ranch Spring Cauldron 2, bones of *Mammuthus*, *Equus*, *Camelops*, *Hemiauchenia*, and *Bison* were recovered from the base of the spring cauldron. Although the fossils appear to have been reworked through artesian activity, they are located stratigraphically below a well-developed organic black mat that yielded a radiocarbon date of 10,560 ± 100 BP (de Narvaez, 1995). The presence of organic black mats near the base of Gilcrease Ranch Spring Cauldron 2 and the dates obtained from these mats suggest affinity with Unit E_2 of the Las Vegas Formation of Haynes (1967) (de Narvaez, 1995), which immediately overlies the late Pleistocene bone-bearing Unit E_1 of that formation in the Gilcrease Ranch area (Haynes, 1967:94). If the fossils at the base of Gilcrease Ranch Spring Cauldron 2 are reworked from the immediately underlying Unit E_1, which seems not unreasonable, then *Bison* might have been present in the Las Vegas Valley between approximately 14.7 Ka and 11 Ka. Coupled with the records of *Bison* from Unit B_2 (144–89 Ka; Page et al., 2005) and Unit D (<31 Ka, probably between ~19 Ka and ~17 Ka; Haynes, 1967; Quade et al., 2003), it appears that *Bison* was present in all fossil-bearing units of the Las Vegas Formation from as early as before 144 Ka through to the end of the Pleistocene.

The observed date range of *Bison* from the Mojave Desert documented here conforms well to recent revisions of the duration of the Rancholabrean NALMA (Sanders, 2002; Bell et al., 2004). The perceived infrequency of *Bison* in later Pleistocene faunas from the region likely results in part from later, but not latest, Pleistocene assemblages having been erroneously referred to the Rancholabrean NALMA on the basis of interpretations that this age was as old as approximately 450 Ka (e.g., Reynolds, 1991; Reynolds et al., 1991a) to approximately 500 Ka (e.g., Jefferson, 1991a). For example, later

Pleistocene localities such as Bitter Springs Playa, Lake Tecopa, and Valley Wells, which have yielded relatively abundant and diverse large mammal fossils (Table 1), were referred to the Rancholabrean NALMA (explicitly or implicitly) despite lacking remains of *Bison* (Reynolds, 1991; Reynolds et al., 1991a; Reynolds and Reynolds, 1994). We propose that the absence of fossils of *Bison* from the above-named localities can be ascribed to fossil accumulation before the appearance of *Bison* in the Mojave Desert region, or at a time when *Bison* was not yet established in sufficient abundance to be manifest in the fossil record. This hypothesis is also proposed to explain the absence of fossils of *Bison* from Unit C at Lake Manix. It is noted in this context that the bone-bearing sediments at Valley Wells have been estimated to range between 50 and 250 Ka in age (J. Quade, personal communication), which, if confirmed, would fit with the results of this study.

It is important to point out that the date of the first appearance of *Bison* in North America south of the glacial ice is not necessarily the date of the beginning of the Rancholabrean NALMA in the Mojave Desert. This might appear to some as a novel concept, because many of the studies conducted on late Pleistocene fossils in the Mojave Desert explicitly or implicitly followed interpretations presented by Kurtén and Anderson (1980), Savage and Russell (1983), or other authors describing NALMAs on a continent-wide basis. However, NALMAs are defined in faunal terms (Wood et al., 1941; Savage, 1951), and faunas do not manifest themselves across the entirety of a continent in a geologic instant (Lundelius et al., 1987; Repenning, 1987; Repenning et al., 1995; Bell et al., 2004; Scott, 2004). Rather, the various index species employed to define NALMAs can appear in different geographic regions at different times, depending on the dispersal patterns of the species in question. NALMAs are thus time-transgressive units. This is important for defining NALMAs in particular geographic regions, for as noted by Repenning et al. (1995:11), "[o]ne can hardly select a mammal age boundary at a time when there is no change in the mammal fauna." In the case of the Rancholabrean, this diachronous nature is more readily perceived than for other, earlier mammal age transitions because of the abundance of Pleistocene localities and the precision of radiometric dating techniques.

For these reasons, we propose that it is a questionable practice to assign vertebrate faunas to a land mammal age if index taxa for that age are not present in the faunas. Such assignments imply a precision that is lacking, consider land mammal ages to be time terms rather than faunal terms, and ignore the time transgressive nature of land mammal ages. In the absence of radiometric dates and index taxa, general terms such as "middle Pliocene" or "later Pleistocene" are preferable to overly precise land mammal age assignments.

As noted previously, the fossil magnum of *Bison* from Twentynine Palms has not been directly dated. The age of this specimen was discussed by Jefferson (1992) on the basis of inferences about the stratigraphy of sediments in the region. Exposures of the Bishop Ash (~758 Ka) were tentatively identified from the Greenish Sand Member low in the section of the Twentynine Palms Formation (Bacheller, 1978). The fossil of *Bison* was recovered from near the top of a second formation, the Campbell Hill Formation, in the Twentynine Palms region (Bacheller, 1978). Jefferson (1992) suggested that the ash horizon from low in the section of the Twentynine Palms Formation might correlate with the lowest exposures of the Campbell Hills Formation. Thus, the fossil from Twentynine Palms was suggested to possibly approach the age of the older "*Bison*" fossils from Lake Manix (Jefferson, 1992). However, because no valid record of *Bison* comes from low in the section at Lake Manix, the Bishop Ash has not been identified from the Campbell Hill Formation, and that furthermore nearly 1,000 feet of section separate the fossil of *Bison* from the base of the Campbell Hill Formation (Bacheller, 1978), no reasonable interpretation of the age of the fossil can be advanced. Although this fossil cannot be stated to conform to the observed age distribution for *Bison* described here, the lack of a date for the fossil precludes rejection of the hypothesis.

ABUNDANCE OF *BISON*

With the exception of records of *Bison* from Unit B_2 of the Las Vegas Formation, and possibly from Twentynine Palms, all records of this genus from the Mojave Desert are younger than about 35 Ka in age. In these younger faunas, remains of *Bison* are generally well represented. At China Lake, *B. antiquus* is estimated to comprise 11% of the fauna on the basis of the number of identified specimens (NISP; Jefferson, 1992). *Bison* makes up approximately 17% of the fauna from Unit E_1 of the Las Vegas Formation on the basis of the NISP (extrapolated from de Narvaez [1995]). At Dove Spring Wash, there are two individuals of *Bison* out of 11 individuals of large mammals on the basis of the minimum number of individuals (MNI), yielding a percentage of approximately 18%, although the small sample size precludes a confident interpretation of the actual abundance of *Bison* in the living population.

At Lake Manix, only one specimen of *Bison* is confirmed from the assemblage. However, Unit D of the Manix Formation is more restricted than the underlying Unit C of that formation in terms

of both its duration and its exposure at Lake Manix (Jefferson, 1968). The temporal and geographic restriction of Unit D might be manifested in the overall faunal abundance from Lake Manix, in that the bulk of the fossil sample from the site has been recovered from Unit C of the Manix Formation. Jefferson (1968) reported only a few large mammal taxa (*Equus* [large and small], *Camelops*, *Ovis*, and *Bison*) from Unit D. The infrequency of fossils of *Bison* from the younger beds at Lake Manix might be an artifact of the reduced numbers of localities from Unit D.

Fossils of *Bison* from Unit B_2 of the Las Vegas Formation at Tule Springs in the Las Vegas Valley (Mawby, 1967) are estimated to date to between 144 and 89 Ka (Page et al., 2005). Remains of *Bison* are estimated to compose 12% of the fauna from this unit on the basis of the NISP (Jefferson, 1992). However, extinct *Bison* from this unit is represented in part by two nearly complete skeletons (Mawby, 1967), whereas other taxa had less complete representation (Simpson, 1933; Mawby, 1967). The published proportion of *Bison* to other large mammals (Jefferson, 1992) probably overestimates the actual abundance of *Bison* in the fauna.

The pattern observed in the Mojave Desert indicates that *Bison* was less well represented in vertebrate faunas than in assemblages from more coastal and inland areas of Southern California. At Rancho La Brea, for example, *Bison* is the most common large ungulate, representing roughly 50% of the large ungulate fauna (according to the MNI); these deposits date to between about 38 and 12 Ka (after Stock and Harris, 1992; Shaw, 2001). Fossils of *Bison* are less well represented at Costeau Pit, another coastal site, where the MNI (10) is approximately 22% of the large ungulate fauna (after Miller, 1971); this locality is older than 40 Ka (Miller, 1971). At Diamond Valley Lake, an inland deposit in southwestern Riverside County (Springer and Scott, 1994; Scott, 1997; Springer et al., 1998, 1999, 2007; Anderson et al., 2002), *Bison* is present in fluvial and lacustrine deposits that range in age from 41.4 Ka or more to approximately 11 Ka (Springer and Scott, 1994; Springer et al., 1999; Anderson et al., 2002). Although analysis of this fauna at the SBCM is ongoing at the time of this writing and final estimates of species abundance are unavailable, preliminary specimen counts suggest that fossils of *Bison* compose as much as approximately 32% of the large ungulate fauna (according to the NISP) from this locality. At the Maricopa asphalt deposits in inland Kern County, *Bison* makes up approximately 25% of the large ungulate fauna (MNI = 10; Torres, 1989), whereas at the nearby McKittrick asphalt deposits, *Bison* composes only 7% of the large ungulate fauna (MNI = 9; Torres, 1989). The Maricopa deposits range in age from approximately 36 to 13 Ka, whereas the McKittrick fossils date to between approximately 38 and 12 Ka (Torres, 1989).

The apparent pattern for coastal and inland late Pleistocene vertebrate localities, as well as for localities in the Mojave Desert, is that *Bison* was present in varying abundance at virtually all localities (excluding cave localities; see below, under "late Pleistocene Mojave Desert Localities Lacking *Bison*") with sufficient numbers of individuals and diversity of large mammal species to constitute a reliable sample, with dates between approximately 40 Ka to the end of the Pleistocene. This distribution pattern is interesting in that it can also be likened to that reported from Texas and the southern Great Plains region (Dalquest and Schultz, 1992; Wyckoff and Dalquest, 1997). In this area, "bison remains appear to be nonexistent in deposits older than 50,000 BP. Moreover, most localities older than 20,000 BP yield more remains of herbivores other than bison" (Wyckoff and Dalquest, 1997:5). Thus it appears that, in portions of the southwestern United States as well as in the southern Great Plains, *Bison* was most abundant in localities of latest Pleistocene age.

This temporal distribution of *Bison* in the Mojave Desert appears to contradict the results of a recent study (Shapiro et al., 2004) that employed Bayesian coalescent theory applied to genetically determined evolutionary divergence dates and proposed a "boom–bust" cycle for late Pleistocene bison populations. In this interpretation, an exponential expansion of the bison population was followed by a rapid decline, with a transition around 37 Ka and an inferred dramatic decrease in bison abundance thereafter. This trend appears to be the exact reverse of the pattern observed in the Mojave Desert on the basis of relative abundance of fossils of *Bison* in late Pleistocene faunal assemblages. However, it is important to note in this regard that these two studies are sampling entirely different bison populations. Shapiro et al. (2004) examined Beringian bison, and although their sample size was extensive, their most southerly data in North America was acquired from Natural Trap Cave in northernmost Wyoming. Reconciling the results of this more northerly study with the data presented here will require a more detailed understanding of bison systematics, phylogeny, and dispersal patterns, particularly in the American southwest. Interestingly, the fossil record of the northern Great Basin appears to lend some support to the conclusions of Shapiro et al. (2004). The American Falls Local Fauna (Pinsof, 1992) is dominated by fossils of extinct bison, but in younger faunas from the region, such as the Duck Point Local Fauna (Hearst, 1990), bison are less abundant relative to camels (*Camelops*), and they are represented by fewer species.

LATE PLEISTOCENE MOJAVE DESERT LOCALITIES LACKING *BISON*

Some late Pleistocene localities from the Mojave Desert are geologically young enough to contain *Bison* (according to our interpretation) on the basis of radiometric dates and have reportedly yielded abundant remains of several large mammal taxa, yet lack fossils of *Bison* altogether. Vertebrate fossils from Kokoweef Cave (SBCM 1.11.13) have yielded a radiometric date of 9,850 ± 160 BP (Reynolds et al., 1991c). The Kokoweef Cave fauna is in part early Holocene on the basis of this date, but extinct taxa are confined to those stratigraphic levels of this Cave beneath the stratum that yielded the date (Reynolds et al., 1991c). (Another fossil-bearing cave in the vicinity, Antelope Cave [SBCM 1.10.10], has also yielded remains of large mammals [Reynolds et al., 1991d], but these fossils are fragmentary and few in number. Furthermore, Antelope Cave had been emptied of its contents by the time paleontologists arrived, so excavation and fossil recovery at this site were restricted to a talus slope outside the cave [Reynolds et al., 1991d]; for this reason, the mode of fossil accumulation of Antelope Cave, and the actual original abundance of fossils, are not known.) At Kokoweef Cave, fossils of large mammals are proposed to have been deposited either by the animals themselves entering the cave bodily (in the case of *Odocoileus* Rafinesque, 1832, and *Antilocapra* Ord, 1818, for which some articulated remains were recovered) or carried therein piecemeal by wood rats (in the case of *Equus* and *Camelops*, represented by isolated pedal elements) (Reynolds et al., 1991c). Pleistocene *Bison*, like present-day representatives (Nowak, 1991), were not commonly mountain-dwelling animals, so they are probably unlikely to have entered either cave bodily. Furthermore, individuals of *Bison* require abundant water and forage, so they probably lived in more open expanses near rivers, streams, and lakes where both food and water were plentiful. This habitat preference would have placed these animals at some geographic distance from Antelope and Kokoweef Caves, and it is unlikely that wood rats would have journeyed so far from their homes or carried such heavy elements as bones of *Bison* over such long distances. It therefore seems reasonable to suggest that environmental factors are responsible for the lack of *Bison* fossils from these caves.

Another possible exception is a record of abundant large mammals from the Yermo region of the Mojave Desert. Reynolds and Reynolds (1985) reported a rich vertebrate fauna from the Calico Lakes site (SBCM 1.76.35) near Yermo that included large *Equus*, *Camelops* cf. *C. hesternus*, *Hemiauchenia macrocephala* (Cope, 1893), and *Ovis canadensis* Shaw, 1804. In this fauna, *Camelops* cf. *C. hesternus* was "the most abundant large mammal with a minimum of twelve individuals" (Reynolds and Reynolds, 1985:186). The fauna was associated with a ^{14}C date of 12,800 ± 900 BP (Reynolds and Reynolds, 1985). According to the results of this study, this is a fauna where one could reasonably expect to find fossil remains of *Bison*. However, examination of the collection reveals that the published report overestimates the number of individuals of *Camelops* present. In fact, only a few skeletal elements of *Camelops* (primarily vertebrae, but with some broken limb elements as well) were recovered, and no duplication of elements was observed. Only two individuals are probably represented: one adult and one juvenile. Review of field notes associated with the project confirmed that the fossils of *Camelops* were found in relatively tightly concentrated loci, reinforcing this interpretation. Each fossil jacket was assigned a different field number, however, and this might have led to some confusion about the number of localities and therefore about the number of individuals present (R.L. Reynolds, personal communication). In any event, the late Pleistocene fauna from SBCM 1.76.35 is very much like that of other localities from around Yermo and Daggett, in that the large mammal taxa are represented by relatively few elements, many of which are fragmentary. We anticipate that fossil remains of *Bison* might be very likely to be recovered from this region at some point, given continued excavation; but the absence of this taxon at present is likely an artifact of preservation and sampling.

A small late Pleistocene vertebrate fauna from Glendale, Nevada, in the eastern Mojave Desert was first identified in 1937 by National Park Service personnel during surveys of the area north of Lake Mead. The assemblage was recovered from gypsum-rich lacustrine, floodplain, and spring deposits in Meadow Valley Wash, and it was located stratigraphically above a reported radiocarbon date of more than 33 Ka (Van Devender and Tessman, 1975). A recent preliminary review of this fauna (Scott et al., 2004) determined that the large mammal fauna consists primarily of postcranial remains; fossils of *Odocoileus* are numerically most common, followed in decreasing abundance by remains of *Ovis*, *Camelops*, *Mammuthus*, and *Equus*. *Camelops* and *Odocoileus* are represented by a minimum of two individuals; for the remaining large mammals, the MNI = 1. The most common animal in the mammal fauna is *Castor canadensis* Kuhl, 1820, represented by several dozen fossils and at least seven individuals, including juveniles, subadults, and adults. *Bison* is not present in this fauna, but because the fossils were recovered stratigraphically from above a horizon whose age is essentially beyond the range of radiocarbon dating, the actual age of the fauna is indetermi-

nate, and the absence of *Bison* might not be unexpected. Ongoing studies of this poorly known fauna might help provide clarification of the age of the fossils.

CONCLUSIONS

1. Fossils of extinct *Bison* are extremely rare from the Mojave Desert, more so than has previously been suggested (Jefferson, 1991a, 1991b) because many of the previous records were in error. The observed infrequency of *Bison* contrasts sharply with the relative abundance of other large mammals from late Pleistocene localities in the Mojave Desert, as well as with the observed abundance of this genus at coastal and inland sites.
2. The rarity of *Bison* in fossil faunas from the Mojave Desert is in part an artifact of earlier interpretations of the extent of the Rancholabrean NALMA. *Bison* appears to have been present in the region after approximately 144 Ka and relatively abundant (although not as abundant as in lower elevation habitats) in all localities (exclusive of cave sites) that have adequate sample sizes and that date between about 40 and 11 Ka.
3. The absence of *Bison* from some later, but not latest, Pleistocene localities with large sample sizes could be because those fossils predate the arrival of *Bison* in the region. Radiometric (accelerator mass spectrometry, electron spin resonance, thermoluminescence) dating of fossils and sediment samples from the Mojave Desert that have not yet been dated, or that are beyond the limits of conventional radiocarbon dating, will help to test this hypothesis. Determining the timing of the appearance of *Bison* in the Mojave Desert has important implications for understanding the evolution and eventual extinction of the large mammal community present in the area during the latest Pleistocene.

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Congenital scoliosis in *Smilodon fatalis* (Mammalia, Felidae) from Rancho La Brea, Los Angeles, California

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ABSTRACT. Abnormal lateral curvature of the vertebral column is a pathologic condition called scoliosis. A series of associated thoracic vertebrae of the sabertoothed cat, *Smilodon fatalis*, from the late Pleistocene Rancho La Brea asphalt deposits in Los Angeles, California, exhibits pathologic characters that represent congenital scoliosis. This is the first case of this malady that has been reported in an extinct mammal. The specimens date to between 28,000 and 33,000 BP and are from the Rancholabrean North American Land Mammal Age.

INTRODUCTION

Scoliosis, the lateral curvature of the vertebral column, is not uncommon in humans (Neuwirth and Osborn, 2001), and it is categorized by orthopedists on the basis of etiology of the deformity. In up to 85% of human cases the cause is unknown, so the most common type of the condition is called idiopathic scoliosis, and at the time of diagnosis it is classified according to the ontogenetic age of the individual: infantile, juvenile, adolescent, and adult (Neuwirth and Osborn, 2001). The remaining cases fall into one of three categories of known etiology: neuromuscular, degenerative, and congenital scoliosis. Neuromuscular scoliosis is caused by one or more neuromuscular diseases (e.g., poliomyelitis), which result in the malfunction of nerves and/or muscles around the spinal column. Degenerative scoliosis is the result of progressive degenerative osteoarthritis affecting the intervertebral discs and pre- and postzygapophyses, which causes eventual loss of support along the spinal column; it is primarily found in older adult individuals with no previous history of idiopathic scoliosis. Congenital scoliosis is a condition that is present at birth, resulting from developmental defects that prevent normal segmentation of the sclerotomes and/or formation of certain parts of the spinal column. Even though a cause has been identified for congenital scoliosis, the mechanism involved is not yet clearly understood. In humans, congenital scoliosis is often diagnosed only after the child reaches between two and five years of age, and it is often associated with kidney dysfunction, urinary-tract abnormalities, or congenital heart defects (Neuwirth and Osborn, 2001).

The uniqueness of the late Pleistocene (Rancholabrean) asphalt-preserved fossil accumula-

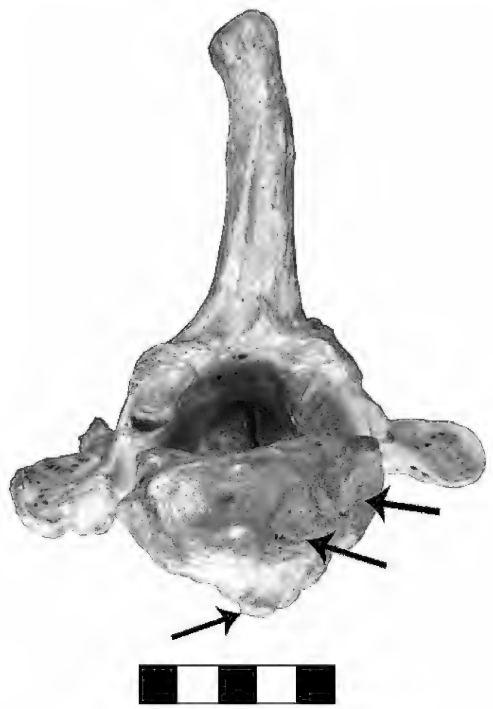

Figure 1 *Smilodon fatalis*, posterior view of the second thoracic vertebra, LACMHC N5563; note the hypertrophic right postzygapophysis and rib facet with subchondral pitting (right arrow), and the spondylosis (left arrow) and eburnation (middle arrow) on the centrum. Scale bar = 5 cm.

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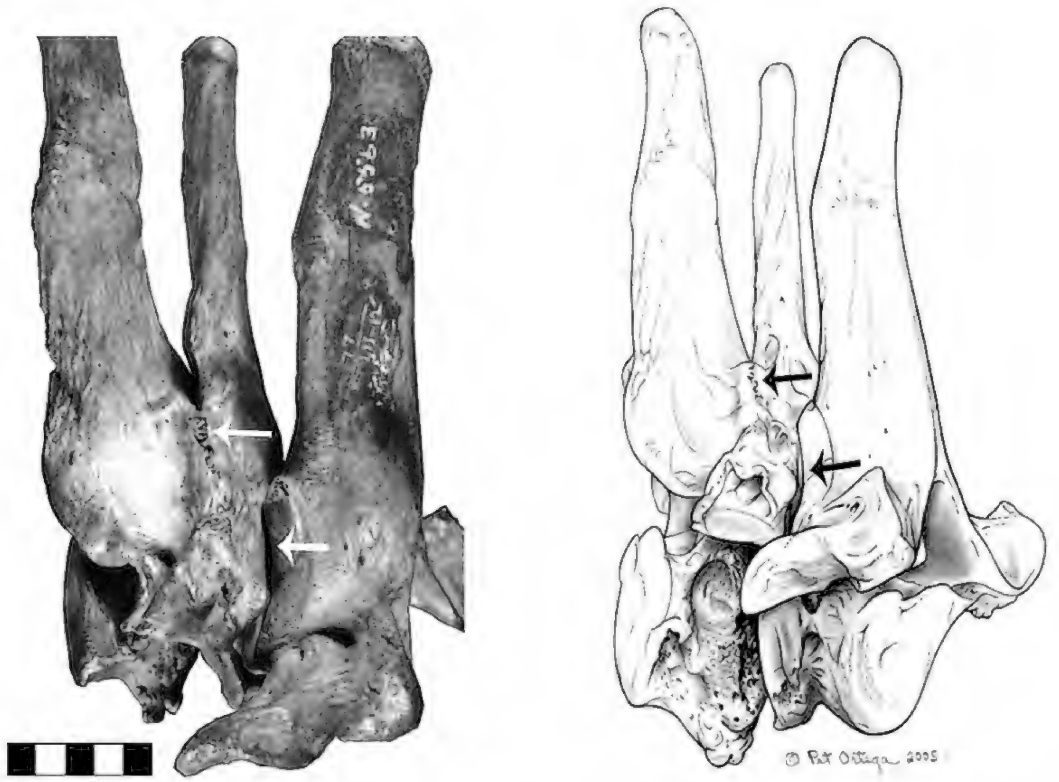

Figure 2 *Smilodon fatalis*, right lateral view of the associated second through fourth thoracic vertebrae, LACMHC N5563 and LACMHC 278, exhibiting the suturelike fusion between the third and fourth thoracic vertebrae (top arrow) and the absence of a transverse process and intervertebral notch of the third thoracic vertebra (bottom arrow). Scale bar = 5 cm.

tions at Rancho La Brea is well documented (e.g., Akersten et al., 1983; Shaw and Quinn, 1986; Stock and Harris, 1992). Excavations were conducted by the Natural History Museum of Los Angeles County (LACM) from 1913 to 1930, during which time over 1 million vertebrate fossils were exhumed. This portion of the fossil collection, along with a large collection that was acquired by the Southern California Academy of Sciences from 1907 to 1910, composes the Hancock Collection (HC), which is housed at the George C. Page Museum of La Brea Discoveries (GCPM). The specimens described here were recovered from Pit 77 in 1915. The taxonomy follows that of Churcher (1984).

Skeletal elements of *Smilodon fatalis* (Leidy, 1868) in the Hancock Collection number approximately 166,000 (Shaw, 2001), and this species represents the second most common large mammal from Rancho La Brea. More than 5,100 of the *S. fatalis* bones (<1%) exhibit some sort of paleopathologic condition (and often multiple abnormalities), and they have been maintained as a separate collection at the GCPM.

DESCRIPTION

The second thoracic vertebra, LACMHC N5563, is associated with fused third and fourth thoracic vertebrae, LACMHC 278, and together these represent a small segment of the vertebral column from a single individual of *Smilodon fatalis*. The centrum and neural arch of the second thoracic vertebra are angulated (i.e., sharply bent) from right to left, anteroposteriorly. Two exostoses, reminiscent of spondylosis, occur on the posteroventral part of the centrum; the posterior articular surface of the centrum is heavily eburnated (i.e., an eroded, highly polished surface created by bone-on-bone abrasion), exposing cancellous tissue near the right ventral margin (Fig. 1). In addition, the neural spine is angulated to the left, the right postzygapophysis is hypertrophic and about three times the size of the left, and the right posterior rib facet for articulation with the third rib is also enlarged and exhibits subchondral pitting.

The conjoined third and fourth thoracic vertebrae are fused along their neural arches at the

Figure 3 *Smilodon fatalis*, ventral view (**a**, photograph; **b**, illustration) of the associated second through fourth thoracic vertebrae, LACMHC N5563 and LACMHC 278; note the left hemicentrum of the third thoracic vertebra (top arrow) and spondylosis on the centra of the second (left arrow) and fourth (right arrow) thoracic vertebrae. Scale bar = 5 cm.

right transverse process of the fourth thoracic. The right transverse process of the third thoracic vertebra and the right intervertebral notch, which conducts the fourth thoracic intercostal nerve, evidently never developed. Between the neural spine and the fused area of the right transverse process, the neural arches of the third and fourth thoracic vertebrae meet to form a suturelike articulation (Fig. 2). The right half of the centrum of the third thoracic vertebra did not develop; the left half of this vertebra is triangular in ventral view (Fig. 3). This hemicentrum and the neural arch of the same vertebra are angulated from

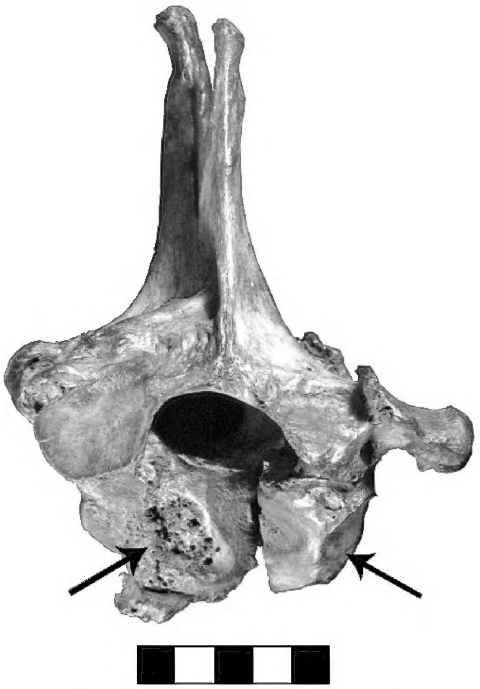

Figure 4 *Smilodon fatalis*, anterior view of the fused third and fourth thoracic vertebrae, LACMHC 278, showing the left hemicentrum (right arrow) of the third thoracic vertebra and the heavily eburnated centrum (left arrow) of the fourth thoracic vertebra. Scale bar = 5 cm.

right to left, anteroposteriorly. Those same structures in the fourth thoracic vertebra are angulated from left to right, which (together with the second and third thoracic vertebrae) served to straighten the spinal column and thus compensated for the loss of the right half of the centrum of the third thoracic vertebra. Exostoses, reminiscent of spondylosis, occur ventrally on the anterior centrum of the fourth thoracic vertebra (Fig. 4). The anterior articular surface is heavily eburnated, exposing cancellous tissue near the right ventral margin. This spondylosis and eburnation coincides with that observed ventrally on the posterior part of the centrum of the second thoracic vertebra. In addition, the right prezygapophysis of the third thoracic vertebra and the right anterior capitular rib facet are as enlarged as the corresponding structures on the second thoracic vertebra, and the left postzygapophysis of the fourth thoracic vertebra apparently never developed. The hypertrophic right rib facets of the second and third thoracic vertebrae together (Fig. 5) might have been enlarged to accommodate the capitulae of both the second and third costal ribs. As viewed dorsally (Fig. 6), the curvature of the three vertebrae is convex to the left side.

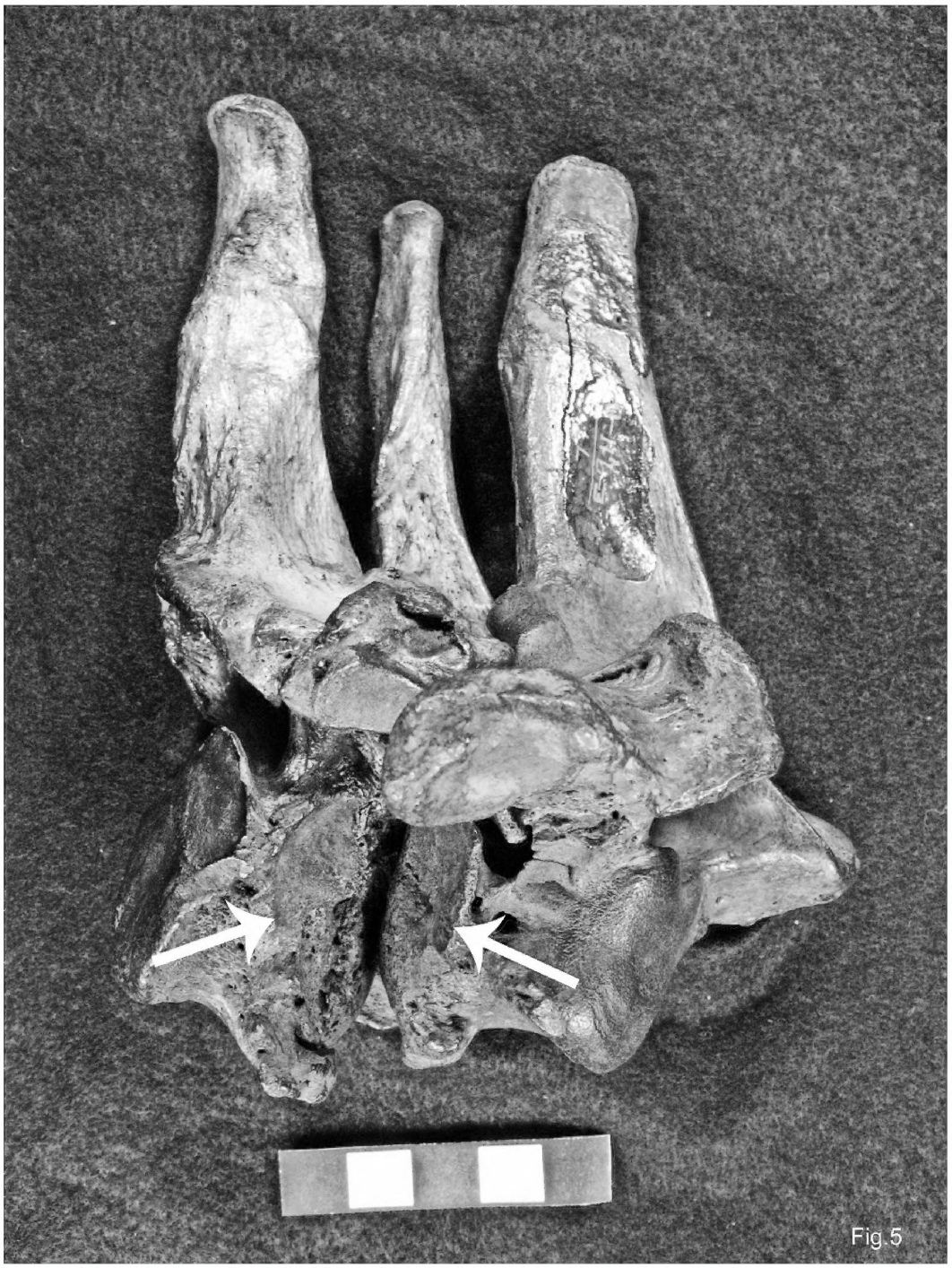

Figure 5 *Smilodon fatalis*, right lateral view of the associated second through fourth thoracic vertebrae, LACMHC N5563 and LACMHC 278, showing the hypertrophic rib facets (arrows) that might have accommodated both third and fourth costal ribs. Scale bar = 5 cm.

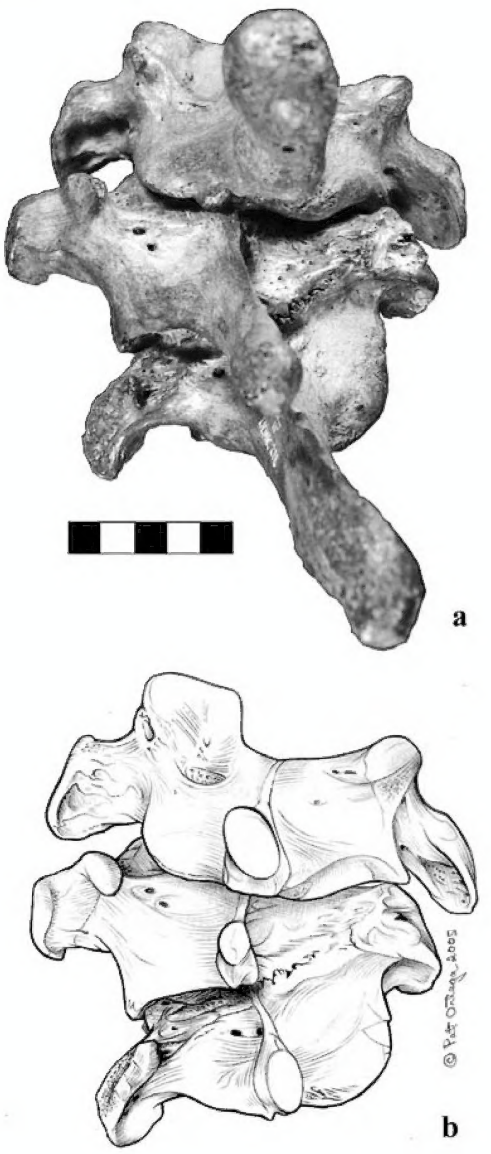

Figure 6 *Smilodon fatalis*, dorsal view (**a**, photograph; **b**, illustration) of the associated second through fourth thoracic vertebrae (anterior at top), LACMHC N5563 and LACMHC 278, demonstrating that the curvature is convex to the left side. Scale bar = 5 cm.

DISCUSSION

Spinal malformations (including scoliosis) are rarely documented in the paleopathologic literature. Ortner and Putschar (1981) attribute this to poor preservation of articulated human vertebral columns relative to other osteological material, and they believed that these defects would be difficult to detect during excavation of an archaeological site. Shands and Eisberg (1955) predicted that scoliosis occurs in less than 2% of the human population of European origin, and the number of known vertebral columns exhibiting marked bone changes is very small (Brothwell, 1967). Of the few published cases of scoliosis, most fall into the idiopathic category; however, in his review of five published and unpublished cases in British skeletons, Brothwell (1961, 1967) attributed one to congenital scoliosis on the basis of the presence of two hemicentra on the third and fourth thoracic vertebrae, and he noted intervertebral disc problems and degenerative osteoarthritis on 11 other associated vertebrae. This skeleton was from the Beaker Period (Bronze Age, ca. 2000 BC) and is the earliest record of congenital scoliosis yet found in humans. In their recent summary of the paleopathologic literature for nonhuman fossil vertebrates, there was no mention by Rothschild and Martin (1993) of any category of scoliosis. However, hemicentra have been found that indicate congenital scoliosis occurred in Jurassic hypsilophodontid and Cretaceous hadrosaurid ornithopod dinosaurs (Tanke and Rothschild, 1997, 2001).

The presence of the hemicentrum on the third thoracic vertebra of the *Smilodon fatalis* specimen (LACMHC 278) is a developmental anomaly that is typical of congenital scoliosis, rather than a condition that was induced by trauma or infection. The degenerative osteoarthritic responses (spondylosis, pitting, and eburnation) on the centra indicate that this individual had attained maturity before it died, and it was not incapacitated by this scoliotic condition.

The Rancho La Brea specimens exhibiting congenital scoliosis were recovered from Pit 77 at a depth of 3.4 to 3.7 m (11–12 feet). Bone collagen extracted from several *Smilodon fatalis* femora recovered from Pit 77 were radiocarbon dated with the use of amino acids that were prepared following the methods of Ho et al. (1969). One femur from a depth of 2.7 to 3.4 m (9–11 feet) yielded a date of 28,000 ± 980 BP; another from a depth of 4.0 to 4.6 m (13–15 feet) resulted in an age of 33,000 ± 600 BP (Marcus and Berger, 1984). Although stratigraphy at Rancho La Brea is not strictly uniform, it seems reasonable that LACMHC N5563 and LACMHC 278 fall within the approximate 5,000-year period that is bracketed by these radiocarbon-dated femora, or between 28,000 and 33,000 BP.

CONCLUSIONS

1. An associated series of second through fourth thoracic vertebrae representing a single individual of the Pleistocene sabertoothed cat, *Smilodon fatalis*, recovered from Pit 77 at

Rancho La Brea, Los Angeles, California, represents a classic case of congenital scoliosis.
2. Although scoliosis in general is not uncommon in living human populations, congenital scoliosis is relatively rare, and only one case has been reported in the archaeological record.
3. The case documented here of *Smilodon fatalis* is the first occurrence of congenital scoliosis that has been reported in an extinct mammalian species, and although it is not the oldest fossil vertebrate account, it is the oldest mammalian occurrence of this malady in the fossil record.

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